USING MULTIVARIATE CALIBRATION TO EVALUATE HOMININ BRAIN/BODY SIZE RELATIONSHIPS

BY

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DISSERTATION

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Abstract

Modern humans are highly encephalized, having relatively large brains despite our already large bodies. The current assumption is that brains and bodies have both increased in size during the course of human evolution but the rate, timing, and evolutionary relationship of the two are still unclear. This study uses methods that increase the sample size of fossil hominins, provide more confidence in body mass estimates, and allow a comparison of the rate and timing of changes in each trait over the past 4+ million years (mya).

Brains and bodies show different evolutionary patterns over time. Body size actually shows a decrease in the Pliocene while brains are essentially static. This would have resulted in more encephalized hominins. At the beginning of the Pleistocene (ca. 2.6 mya) body size began to increase and brains began a modest but discernible increase. Body size became static about 1.0 mya and brain size increased sharply around 0.4 mya (close to the appearance of the first *Homo sapiens*). These patterns indicate that both traits were subject to differing selection (directional or stabilizing) or genetic drift at different times. Their genetic covariation is low; this trait is also subject to selection so the amount of covariation can change throughout time.

Taken together, these results suggest a complicated relationship between brain size and body size. Both traits were probably experiencing some direct selection, while also susceptible to indirect selection from the other based on their covariation. The dissimilarities in the change of body size and brain size indicate that their covariation was actively changing during the course of human evolution. Other research indicates that humans have less phenotypic integration than great apes. For example, the transition to bipedalism may have been eased by lowering covariation within the hip, thus reducing evolutionary constraint. This pattern of "evolvability" could extend to more general modules or groups of traits, like the skull and brain size, or skeletal and body size.

Changes in selection on brain size and body size would have been rooted in environmental and life history changes; many life history changes accompany brain size and body size changes. If we examine the analyses of the entire sample, Australopithecines were experiencing decreasing body size and relative stasis in brain size, producing an overall result of encephalization. As brains got relatively larger compared to bodies it was inevitable that at some point either brains would have to get smaller along with bodies or bodies would

have to start getting larger to birth large-brained offspring. After 2.6 mya the selection for bigger brains could be responsible for driving larger bodies, but brains show positive allometry relative to bodies. These changing phenotypic relationships suggest changing genetic relationships, indicating a different pattern in integration that began to emerge.

There is still much to learn and understand about the evolution of human brains and bodies. These analyses lend some clarity to the rate and timing of evolution of both brain size and body size over time, but the trends are not directly comparable because body size changes linearly over time while brain size shows an exponential increase. Results support previous findings in many ways, including probable changes in energy allocation to support a large brain, an increased rate of evolution in more recent hominins, and changing phenotypic integration. New results include body size decreasing and brain size stasis in the Pliocene, as well as static body size and increasing brains in the Pleistocene.

To my buddy Daubert.

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Dissertations are typically recognized as individual accomplishments and the process is often isolating and solitary, but in retrospective this dissertation seems as much a group project as anything I have every written, not because others wrote it but because they endured my writing it. I cannot imagine that anyone finishes a dissertation without a huge amount of emotional support from those around them. I know I cannot capture that spirit in these acknowledgements but I will try.

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Chapter 1

Introduction

Brain size has increased both absolutely and relative to body size since the appearance of the human lineage. Absolutely, brains have increased from ca. 400—500cc (*Australopithecus*) to a maximum of over 1500cc during the Upper Palaeolithic (Ruff et al., 1997) and then decreased to a current average volume of 1350—1400cc (Falk, 1991; Ruff et al., 1997). Body mass has also increased over the same period of time, but not as dramatically. As a result, brain size evolution requires a consideration of scaling, which has been difficult to quantify. Small sample sizes pose a serious problem for scholars wanting to analyze fossil hominins, particularly because very few specimens preserve associated cranial and postcranial remains. Small sample sizes lower our statistical confidence in any estimate, and in this case we already have little confidence in size estimates for fossil hominins because they also present a calibration problem—for many species we lack an appropriately similar reference sample.

Studying the brain/body mass relationship in modern humans is straightforward because of the wealth of brains and bodies to measure. Data exists from large, longitudinal health studies, medical examiners, as well as recent, well-preserved archaeological specimens. However, research on fossil material faces many hurdles: fragmented analyses of geological time, incomplete data, and unreliable estimates of body and brain size. My research approaches this question by generating better estimates of fossil hominin brain size and body mass and then modelling those estimates across geological time. Humans' brains are relatively very large even when compared to most of our fossil ancestors and extant ape relatives. It remains unknown at what point in human evolution increasing brain size began to outpace increasing body mass. A clearer resolution of the mechanism, rate, and timing of relative brain size increase has implications for understanding long-standing problems in human evolution ranging from the morphological correlates of bipedal locomotion and giving birth to large infants, to diet, ecology, anatomical changes to other organs, and life span.

This project proposes a way to quantify the relationship between brain size and body mass even when 1. individual specimens have an estimate of only one of these measurements and/or 2. the available (modern human) reference sample differs from the target specimen significantly enough to require extrapolation. A better estimate of the relationship of brain size to body mass and how it changed over time will lay the foun-

dation for insight into profound questions in human evolution: how and when did humans (or our ancestors) dramatically increase brain size relative to our body mass? What evolutionary mechanisms underlie the ability to overcome brain size constraints? What ecological or biological variables drove encephalization?

1.1 Relative Brain Size

Any measure of relative brain size requires accurate estimates of both brain size and body mass, which is the first task of this research. I used multivariate calibration as a means to obtain body mass estimates of fossil hominins with a measured (and tempered) amount of confidence. These methods have been previously applied to fossil hominin stature (Konigsberg et al., 1998; Hens et al., 2000) and have only recently been used for estimating fossil hominin body mass (Uhl et al., 2013). The calibration processes allow for a tailored estimate for each fossil specimen depending on how many postcranial measurements are available and how similar the specimen is to the modern human reference sample. Endocranial volume (EV) is used as a proxy for brain size. I did not estimate EV for fossil hominins, but rather I culled reported EVs from the paleoanthropology literature.

While some have argued that overall brain size, rather than relative brain size, is the most important cognitive variable (Deaner et al., 2007), most agree that a consideration of brain size as a percentage (or other measure) of body size is important. Relative brain size has been studied since the 19th century (Schmidt-Nielsen, 1984); major data synthesis for vertebrates and mammals is credited to Jerison (1973) and Martin (1981). The data show interspecific scaling values of brain size to body size at $\frac{2}{3}$ and $\frac{3}{4}$, respectively. Intraspecific scaling values are much lower (e.g., 0.33) (Pilbeam and Gould, 1974), however, within hominins scaling values are much higher than expected (Pilbeam and Gould (1974) estimate 1.77).

A consideration of both static and evolutionary allometry is important in the analysis of brain size evolution. Allometry is the study of scaling relationships between different body parts. Body parts that genetically covary are subject to change by indirect selection—that is, the body parts are integrated. Because allometry itself is a phenotype with a genetic basis the scaling relationships can be affected by selection and drift. Allometric differences are assessed in three ways: ontogenetic allometry, static allometry, and evolutionary allometry (Cheverud, 1982). Ontogenetic allometry tracks changes in size relationships within individuals as they grow. Selection at different points in the growth trajectory can result in different amounts or sizes of cells, causing divergence of brain size and body mass. It is clear that humans have overcome constraint to grow relatively large brains, but it is currently unknown at what point in our ancestry hominin brain growth exceeded body growth. Static allometry examines differences in size relationships between

individuals in two or more groups (e.g., males and females) at a point in time (e.g., adulthood). Evolutionary allometry assesses the differences in size relationships between species; ontogenetic and static allometry, as well as genetic and environmental factors are assumed to contribute to evolutionary allometry (Cheverud, 1982). More accurate estimates of fossil hominin brain size and body mass could clarify allometric and evolutionary relationships.

Allometric approaches are important, particularly in evolutionary anatomy because of the modularity of organisms. Modularity is a genetic covariance, or integration, that results in the coevolution of phenotypic traits; as a result anatomical changes can occur because of a correlated response to selection, not a direct response to selection (Goodnight, 2006). Considering all three types of allometries prevents an adaptationist approach that assumes all phenotypic changes are a direct response to selection. It requires a critical evaluation of anatomical relationships during ontogeny, patterns resulting from that growth, and how those relationships contribute to evolutionary change (Antón and Leigh, 2003).

1.1.1 Genetic Correlation of Brain Size and Body Size

Underlying genetic covariation results in traits that are phenotypically dependent on each other. The effect is that when there is selection on Trait A, Trait B will change with it, even in the absence of direct selection on Trait B. Evolutionary biologists are only beginning to recognize which traits may not be "adaptive." For example, Rolian (2009) shows that finger length in humans is mostly the result of covariance with toes. As human toes shortened to optimize length for bipedalism, fingers simultaneously shortened in the absence of direct selection because they genetically covary with toes. Further clouding the evolutionary picture is the evolvability of these relationships. Covariation between traits is not static, and in fact, changes in covariation may underlie watershed moments in evolution (e.g., Lande, 1979). Brain size and body mass are genetically positively correlated (Lande, 1979), so selection pressure to increase brain size should result in increased body mass even in the absence of selection for larger bodies. When the rate of increasing brain size surpassed the rate of increasing body mass it could have been accompanied by a reduction in the genetic correlation between brain and body mass. Reduced correlation would relax the constraint that body mass imposed on brain size and brain size could begin to outpace body mass.

Before Lande (1979) applied quantitative genetic methods many assumed that allometric changes were merely the consequence of selection on one character (usually body mass) and the correlated response of brain size. His work indicates that this is probably the case for mice, whose brain size is largely a correlated response to directional selection on body mass. Lande (1979) posited that over the course of primate evolution the genetic correlation of brain size and body mass has decreased significantly. If brain

size and body mass are highly correlated then any change in one produces a change in the other and, without decoupling, encephalization would require either antagonistic selection (simultaneous selection for larger brains and smaller bodies) or would result in gigantism. Following from this, primates have become encephalized because of the low genetic correlation between brain size and body mass and either directional selection or random genetic drift resulting in larger brains.

A series of experiments on mice reinforces that the genetics of growth underlie much of the evolution of large relative brains (Riska and Atchley, 1985). Growth happens by either hyperplasia (adding more cells), or hypertrophy (making existing cells larger)(Goss, 1966). Both intrinsic and extrinsic growth factors contribute to brain and body growth. Several intrinsic factors contribute to hyperplastic differentiation and growth in utero. Instrinsic factors and the genes that produce them are more tissue specific and so affect neural tissue and other tissues (i.e., epithelial, muscle, connective) differently. Neural crest cells are multipotent embryonic cells that differentiate into a collection of adult tissues that seem unrelated. The extrinsic factors have a more widespread effect on tissues but still contribute both to promotion and inhibition of growth and differentiation (Calof, 1995). A change in the timing or amount of extrinsic vs. intrinsic factors could stimulate brain growth in humans/hominins without the same stimulating effect on body growth.

1.1.2 Rate and Timing of Brain and Body Changes During Hominin Evolution

Rate and timing of morphological evolution is difficult to quantify. Most regression procedures have several assumptions that are probably violated when assessing a time series of morphologies. Independence and constant variance are the most obvious violations, but that has not stopped many from using Ordinary Least Squares regression or related methods such as, Reduced Axis and Reduced Major Axis regression to assess brain size or body size over time (e.g., Blumenberg, 1984, 1985; Rightmire, 1981).

Fitting a line severely limits the amount of information one can glean about both the rate and the timing of changes. The line reduces the variance that we are interested in. Another complication is a usually-unstated assumption of phyletic gradualism. This implies a fairly steady change over time, however, a look at the EV data raises questions about this assumption. Eldredge and Gould (1972) published the primary alternative to phyletic gradualism—punctuated equilibrium. Punctuated equilibrium is characterized by changing rates of evolution in a characteristic, including some periods of stasis. Although the EV data, particularly the early specimens, are incomplete, it is difficult to argue for gradualism in brain size increase. Some authors have used non-parametric techniques to identify periods of stasis (Leigh, 1992a; Hawks, 2011).

Additionally, Bookstein et al. (1978) demonstrated that the choice of which species to include and which time period to analyze (what one chooses to look at) will affect which trends manifest in the results. Finally,

when analyzing an evolutionary time series, one cannot assume independence of data points because of the problem of phylogenetic relatedness. There are several measures for correction, most developed by Felsenstein (1985a,b), however, these are based mostly on independent contrasts, which also make assumptions (Pagel, 2002). Pagel (2002) uses a tree model to assess brain size evolution in hominins. While I do not use similar methods it is an interesting exercise to compare his results to mine.

1.2 Evolutionary Trade-offs

Human brains are large even when accounting for our large body mass (relative to other mammals), and because the brain accounts for 20-25% of our resting metabolism (Leonard and Robertson, 1994), many other anatomical and ecological variables must have changed in concert during the evolution of the human brain size/body mass relationship. These include pelvis size and shape, locomotor strategy, diet and nutrition, and life history traits such as gestation length, length and progression of ontogeny, interbirth interval, and others (Aiello and Wheeler, 1995; Isler and van Schaik, 2009).

Brain size and body mass are central to human biology and behavior. Larger brains and larger bodies are both resource-intensive, requiring large amounts of calories, changes in diet and nutrition, and/or concomitant changes to the digestive system. Brain size and body mass also influence the evolution of the pelvis and its role not only in bipedalism but also in birthing larger human heads (e.g., Rosenberg and Trevathan, 1995; Wells et al., 2012). Few authors propose a specific selection pressure, other than that big brains seem adaptive.

One approach to considering the human brain size/body mass relationship is to put it in the context of brain size variation among other animals. Most hypotheses center around perceived benefits of increased brain size like increased cognitive ability (Deaner et al., 2007) or increased sociality (Dunbar, 2009), but because large brains are metabolically expensive and require life history changes to allow for development, an assesment of net benefits (including costs) is important (Isler and van Schaik, 2009).

Aiello and Wheeler (1995) introduced the Expensive Tissue hypothesis, which posits that humans experienced a reduction in gut size concomitant with an increase in brain size. This hypothesis addresses the two ways in which the costs of a large brain can be met: an organism needs to either increase energy intake or change energy allocation (Isler and van Schaik, 2009). Recently, more generalized models have begun to form a broader framework that encompasses more mammals (Jones and MacLarnon, 2004) and birds (Isler and Van Schaik, 2006; Isler and van Schaik, 2009), rather than focusing only on humans and other primates. Isler and van Schaik (2009) term this the Expensive Brain hypothesis; it subsumes the Expensive Tissue

hypothesis. Not surprisingly, some species have tradeoffs other than reduced gut size. For example, birds with larger brains have smaller pectoral muscles (Isler and Van Schaik, 2006). Muscle efficiency, particularly with regard to locomotion, could have played an important role not only in human brain size increases but also in the evolution of obligate bipedalism (Rodman and McHenry, 1980).

Trade-offs for larger brains can also take the form of life history changes. Polytokous organisms typically reduce litter size as brain size increases. Monotokous organisms, like humans, cannot reduce litter size so they tend to increase interbirth interval, length of gestation and development, and overall life span (Isler and van Schaik, 2009). These life history changes combine to alter the patterns, rates, and relationships of growth for organs and overall body mass.

Adult brain and body mass are products of rate and length of growth (ontogeny). Brain size scales with body mass in a predictable way in most mammals (Jerison, 1973) because common biological growth factors underlie their ontogeny (Riska and Atchley, 1985). However humans are uniquely underdeveloped at birth, requiring a long period of care while they grow. Human bodies grow for a much longer period of time than brains (Leigh, 1992b, 2004), and these changes in their rates of growth underlie evolutionary variation in the brain/body mass relationship (McKinney, 2002).

1.3 Current Study

Fossil remains are few, fragmentary, damaged or deformed. Body mass is most often estimated through linear regression and the association of certain postcranial skeletal measurements with overall size. In fossils, the shafts of long bones have a different relationship to body mass than those of modern humans, so articular (joint) surfaces are preferable (Ruff et al., 1997; Uhl et al., 2013). Regardless of which skeletal element is used, issues with estimating body mass for fossil hominins persist because of differences in scaling relationships (Konigsberg et al., 1998). Endocranial volume estimates are the most common proxy for brain size. Values for fossil hominins usually come from previous research without consideration of measurement error, and often without mention of how estimates were obtained. The problems with EV estimates are closely tied to the salient problems in all analyses of fossils: sample size is too small, fragmentary, and biased with regard to time period, sex, and geography.

This research uses a reference sample comprised of cadaveric modern humans (N = 546). These individuals are all known with recorded age, sex, stature and body mass. Each individual has multiple measures of postcranial bones (see Table 3.1) that form the reference sample for estimating body mass of fossil hominins. Access to fossil hominins is difficult so their measurements come from literature sources (see Table 3.2).

These measurements of fossil hominins form the target samples.

My research applies two statistics (R and Rx) from the calibration literature to body mass estimation for the first time. This important step acknowledges the possible difference between the target's body mass or allometry and the mean body mass or allometry of the reference sample (Brown and Sundberg, 1987).

Early fossil hominins fall at the smaller end of the modern human body mass range. Most studies estimate Australopithecine body mass between about 30kg-50kg (e.g., McHenry, 1991, 1992a), but later hominins (i.e., *Homo erectus* and later) achieved mean body mass larger than the mean of modern humans, although they still fall within the range of modern human variation (ca. 65 kg) (Ruff et al., 1997). While mean size of these hominins falls within the modern human body mass range, individual specimens may fall outside of that range; even more plausible is that hominin postcrania scale to body mass differently than the modern human reference sample used to estimate size.

I propose that multivariate classical calibration can mitigate some of the effects of differences in body mass and proportions when estimating body mass. In this context, classical calibration involves regression of a postcranial skeletal indicator of body mass (long bone length or shaft diameter, or articular surface size) on body mass (body mass) followed by solving for body mass. The reference sample probably does not form a reasonable prior but Konigsberg et al. (1998) and Hens et al. (2000) demonstrated that classical calibration provides a reasonable estimate of stature even when it requires extrapolation, so the same should apply for body mass estimation.

This project aims to model and quantify the relationship of brain size to body mass in fossil hominins and modern humans. Brains and bodies have both increased in size, probably at least partly in tandem. Isometry would indicate that brain size increase has been purely a consequence of body mass increase or vice versa. Alternatively, brain size has experienced positive allometry, meaning its increase has outpaced body mass increase. Negative allometry in this context involves a temporal trend of decreasing brain size relative to body mass. Adult brain and body mass is a product of both rate and length of growth (ontogeny). Because in most animals bodies grow for a much longer period of time (Leigh, 1992b; Cabana et al., 1993) than brains (Leigh, 2004), one would presume that negative allometry is the most likely outcome given this situation, so it is of interest if modern humans and fossil hominins were able to overcome this.

Does the benefit of a big brain outweigh that of efficient bipedalism or a relatively easy birthing process? The current understanding of the fossil record is that bodies and brains became human-like ca. 2 mya (Leigh, 2004), which is much more recent than the appearance of bipedalism (ca. 4 mya), but the possibility of earlier large relative brains has been subject to relatively little exploration. This is also probably an oversimplification that assumes an unchanging covariation between body size and brain size.

The evolution of the brain size/body mass relationship remains one of the most vexing unanswered questions in human evolution. Models of the mode of evolution driving increasing brain size revolve around directional selection for a host of reasons including sociality (Dunbar, 2009), cognition (Richerson and Boyd, 1999), hunting skills and dietary changes (Aiello and Wheeler, 1995), or climate change (Beals et al., 1984). Lande's (1979) work suggests this kind of intense directional selection on brain size was possible because of a decoupling of genetic correlation of brain size and body mass. Understanding the timing of allometric changes in brain size and body mass relationships is the first step in unraveling how, when, and why humans acquired such large brains.

Chapter 2

Literature Review

Humans' brains are exceptional because even when accounting for body mass they are very large compared to most of our fossil ancestors and extant ape relatives. The timing and mechanism of relative brain size increase in humans and our ancestors remains a mystery. What is apparent is that the process was not as simple as natural selection for "bigger brains are better." A clearer resolution of the mechanism, rate, and timing of relative brain size increase can help parse out the role of selection, genetic drift, ontogeny, and modularity in attaining the modern human form and life history.

2.1 Estimating Hominin Body Size

Although many biological anthropologists study hominins that are long dead, estimating living body mass is a critical step in understanding many other aspects of those hominins' biology, ecology, ontogeny and life history, even given this, Smith et al. (1996) criticized the use of body mass estimates to imply these kinds of traits. As one would expect for such an important trait, myriad estimation techniques have been developed over several decades. The development of a technique involves a choice not only of which skeletal element(s) to include, but also which statistical methods to employ. Lower limb bones are an obvious choice for assessing body mass, especially in fossil hominins, all of whom are presumed to have been bipedal. Because bone responds to mechanical stress, aspects of the lower limb correlate fairly well with body mass. Proposed methods include use of articular surfaces, diaphyseal measurements (both proximal and midshaft absolute and cortical widths, and circumference), and inclusion of long bone length or pelvic dimensions mostly as a way to incorporate stature. Statistical methods are almost always some form of regression using an extant species reference sample to estimate an extinct species target specimen.

The obvious connection between lower limbs and body mass has generated most of the literature on this topic. Jungers (1982, 1984, 1988b, 1990) and McHenry (1976, 1991, 1992a,b) pioneered estimation of body mass for fossil hominins, although most of their focus is on Australopithecines rather than fossil *Homo*. Their techniques are straightforward, generally using postcranial articular surfaces, sometimes including long

bone lengths, and ordinary least squares regression using modern humans and extant non-human primates both in combination and separately. Ruff (1991); Ruff et al. (1994, 1997) and Auerbach and Ruff (2004) have lead the way in estimates for fossil *Homo* and modern human populations. Ruff repeatedly advocates the consideration of body proportions (length and width) in the estimation of body mass. He proposed a cylindrical model (Ruff, 1991; Ruff et al., 1994) where surface area changes as width changes, but not as length changes, although it is not clear that that cylindrical shape applies well to humans. Building on this he compared body mass as estimated by femoral head measurements and a stature/bi-iliac breadth equation (Ruff et al., 1997; Auerbach and Ruff, 2004). The estimates from each technique are highly correlated, however, the stature/bi-iliac breadth measurement requires one to first estimate stature and then use that estimate to estimate body mass, thus piling error on error.

Auerbach and Ruff (2004) juxtapose body mass estimation techniques as either "mechanical" (i.e., articular surfaces, in this case femoral head) or "morphological" (i.e., not mechanically related to weight transmission, in this case stature/bi-iliac breadth) in modern human populations. In this, and previous studies (e.g., Ruff et al., 1997) the authors curiously combine several estimates from each technique. Final femoral head body mass estimates are averages of femoral head body mass estimates based on three or four separate equations (three if sex is known, four if sex is unknown). The practice of averaging estimates disregards the uncertainty inherent in any estimate. The authors make no mention of confidence intervals or standard errors of these estimates, nor do they consider any kind of uncertainty after averaging the estimates. Bi-iliac breadth and stature are both estimated in most cases (unless they can be measured directly as in cadaveric samples) and the authors again fail to report the uncertainty of these estimates or the uncertainty of body mass based on these estimates. The authors conclude by recommending their "morphological" technique (bi-iliac breadth/stature), but the greater utility or accuracy of this method over the "mechanical" technique remains unclear. The application of these techniques to modern humans was an extension of Ruff and colleagues' (1997) use of these methods to estimate body mass in Pleistocene *Homo*. Again, estimates of body mass from femoral head measurements and bi-iliac/stature methods are compared and produce fairly congruent results. However, in the case of these fossils, bi-iliac breadth is undoubtedly estimated and the methods are unclear. The authors cite Ruff's (1994) cylinder model and "knowledge of clinal variation," which implies a best guess rather than scientific rigor. In terms of simplicity, availability, and biomechanical reasoning, the femoral head (and other lower limb articular surfaces) has the most utility in body mass estimation.

Attempts at fossil hominin body mass estimation are statistically disadvantaged in many ways. The most obvious problem is sample size. Fossil hominin post cranial remains do not abound and those that we do

have are often fragmentary, damaged and/or deformed. We have many more cranial and dental remains of fossil hominins, and these remains are more easily classified to the species level, so several methods utilizing these elements exist. Teeth are popular for body mass estimation in other mammals (Damuth, 1990), and have been used for body mass estimation in fossil hominins. Because changes in the masticatory apparatus in fossil hominins seem capable of evolving mostly independent of body mass, this approach failed to gain traction. McHenry (1988) specifically addresses the impact of megadontia in Paranthropus body mass estimation. Other cranial variables show high correlation with body mass within, but not across, primate species. Aiello and Wood (1994) investigated several cranial measurements and found the highest agreement with orbital measurements and biporionic breadth. Kappelman (1996) followed up by digitizing eye orbits and calculating orbital area. Rightmire (2004) employed these orbital measurements in his assessment of relative brain size in *Homo erectus*, and while his methods seem appropriate, the problem with these cranial measurements (and body mass estimation for fossils) is obvious in his 95% confidence interval ranges. For many individuals the ranges are from 30kg to 90kg. This uncertainty is mostly a function of small sample size. Others have argued against the use of cranial variables because weight is not transmitted through the head (Hylander, 1985; Jungers, 1991; Hartwig-Scherer and Martin, 1992; Plavcan, 2003), however, Smith (2002) advocates the use of whatever variable(s) has (have) the least uncertainty statistically, regardless of whether they make sense functionally. Hartwig-Scherer and Martin (1992) caution that cranial variables, despite their mechanical independence from body mass, can scale differently with body mass in different species. Their example of differences in biorbital breadth allometry between *Pan troglodytes* and *Pan paniscus* is a convincing word of caution.

Most body mass estimates cited for early Plio-Pleistocene hominins in the literature are traced back to McHenry (1992a)(see Table 2.1). McHenry (1992a) has an extensive set of postcranial measurements for multiple fossil specimens and uses several regression approaches (Ordinary Least Squares, Major Axis, Reduced Major Axis) with two different reference samples (intrahuman and interhominoid). The reported and most commonly repeated (e.g., McHenry and Coffing, 2000; Wood and Collard, 1999) body mass estimates are based on human proportions.

Table 2.1: Body Mass Estimates from McHenry (1992)

Species	Intrahuman (M\F)	$\bar{x}$	Interhominoid (M\F)	$\bar{x}$	N (M\F)
A. afarensis	44.6\29.3	37.0	60.1\35.6	47.9	3\3
A. africanus	40.8\30.2	35.5	52.8\36.8	44.8	5\7
P. robustus	40.2\31.9	36.1	49.8\40.3	45.1	2\2
P. boisei	48.6\34.0	41.3	76.0\42.0	59.0	1\1
H. habilis	51.6\31.5	41.6	75.0\41.5	58.3	3\2

The body mass of *Australopithecus africanus* is estimated as 41kg for males and 30kg for females (mean = 36kg) (McHenry, 1992a) based on an Ordinary Least Squares (OLS) regression using a modern human sample. As reported in the table, McHenry (1992) also estimated body mass using a hominoid-generated regression equation, which gave drastically different results. The differences are eye-catching and point to a number of potential taxonomic and analytic issues.

Berger et al. (2010) describe a new *Australopithecus* species (*sediba*) found in Malapa, South Africa. These authors argue that *Australopithecus sediba* may be ancestral to the *Homo* lineage, although it is classified as *Australopithecus* in part because of its small cranial capcity (420 cc). Measurements of the humerus and femur are reported. The two specimens (MH1 and MH2) described by Berger et al. (2010) date to about 1.96 mya. The authors have argued that *Australopithecus sediba* shares more derived features (both craniodental and postcranial) with *Homo* and may help clarify the relationship between Australopithecines and *Homo*.

Early Pleistocene fossil hominins are scarce, except for some of the terminal species representing the *Paranthropus* genus. *Paranthropus aethiopicus* is the earliest member of this genus, found in West Turkana and dated to 2.7 to 2.3 mya. Walker et al. (1986) originally attributed KNM-WT 17000 to *Australopithecus boisei* but it was subsequently attributed to *Australopithecus (Paranthropus) aethiopicus* because of its suite of derived characteristics shared not only with *P. boisei* but also with *A. africanus*. The cranial capacity of KNW-WT 17000 is an estimated 410cc (Walker et al., 1986), much smaller than the average estimated cranial capacity for *Paranthropus boisei* (513cc) and *Paranthropus robustus* (530cc) (Collard and Wood, 2007). However, *Paranthropus aethiopicus* predates other *Paranthropus* species by at least 400 ka (Collard and Wood, 2007). There are no postcranial remains, and so no body mass estimate, for *Paranthropus aethiopicus*, but other *Paranthropus* species have estimated body masses of 40.2±15.8kg (male *P. robustus*), 31.9±21.5kg (female *P. robustus*), 48.6±34.6kg (male *P. boisei*), and 34.0±13.7kg (female *P. boisei*) (McHenry, 1992a).

The body mass estimates for *P. robustus* are based on only two individuals for each sex, while the *P. boisei* estimates are based on only one male and one female individual (McHenry, 1992a). These estimates come from OLS regression on hindlimb joint size, assume that *Paranthropus* shared modern human body proportions (this concept is addressed in the following section), and have very large confidence intervals as a result. Dates for *Paranthropus boisei* range from 2.3 mya to 1.4 mya (McHenry and Coffing, 2000); *P. robustus* begins later (1.9 mya—1.4 mya) and co-existed with early *Homo* at the South African Swartkrans site (Susman et al., 2001).

Several authors posit that the Laetoli and Hadar *Australopithecus afarensis* specimens represent two separate species (see references within Richmond and Jungers (1995)). Alternatively, a more accepted view is that *Australopithecus afarensis* could characterize one species that is very sexually dimorphic (Richmond

and Jungers, 1995). Despite the acceptance of this latter view, there is still disagreement about the extent of *A.afarensis* sexual dimorphism. Degree of sexual dimorphism is implicated in several social aspects of primate life, particularly mating patterns, and while those are beyond the scope of this project, the disagreement on body mass is notable. McHenry notes large-sized hindlimb joints from Hadar (1992: 421). Konigsberg et al. (1998) and Uhl et al. (2013) show that at least one *A. afarensis* specimen (A.L. 288-1) differs allometrically from a human reference sample and this has implications for accuracy of body mass estimates, as Neubauer et al. (2012) demonstrated for *A. africanus* EV estimates.

Body mass of *Ardipithecus ramidus* is estimated from ARA-VP6/500, for whom cranial capacity is reconstructed; it is identified (based on canine size) as a female who stood about 120cm (range: 117cm –124cm) and weighed 51kg (Lovejoy et al., 2009). The body mass for ARA-VP-6/500 comes from estimates based on metrics of the capitate and talus. Stature estimates rely on partial long bones and the assumption, for lower limbs, that *Ardipithecus ramidus* has a similar crural index to that retained by extant African apes and humans, and for upper limbs that bones from different *Ardipithecus ramidus* individuals can be substituted for each other, despite size differences based on several shared metrics (Lovejoy et al., 2009, p. 100). Lovejoy et al. (2009) do not address the possibility that *Ardipithecus ramidus* was integrated differently than extant great apes with respect to the relationship between overall size and carpal/tarsal size.

McHenry (1992a) estimated the body mass of male and female *Homo habilis* as 52kg and 32kg, respectively. As with his *Australopithecus* and *Paranthropus* body mass estimates, the *Homo habilis* estimates use a modern human reference sample and so assume modern human proportions. A "hominoid" reference sample produces significantly lower body mass estimates (10kg–23kg for males, 4kg –10kg for females) (McHenry, 1992a).

Body mass of *Homo erectus* has been reconstructed many times for the juvenile specimen KNM WT 15000 (Ruff and Walker, 1993; Graves et al., 2010; Uhl et al., 2013); it is a useful specimen because of its completeness but its juvenility is a serious concern.

Despite my skepticism of Ruff's (1991, 1994) cylinder model, body proportions and allometry are a valid concern in body mass estimation. Estimating body mass for fossil hominins uses the relationship between skeletal measurements and body mass in extant species to estimate the relationship between those skeletal measurements and body mass in extinct species. It is virtually certain that the relationships between skeletal elements and body mass are different in different species (i.e., there are allometric differences). Ruff (1990) found that modern human femoral heads are strongly positively allometric relative to body mass, however his comparison only involved extant non-human primates. The reasoning behind the strong positive allometry

is that human bipedality applies more mechanical stress to the femoral head. If bipedality is, in fact, the reason for this positive allometry then it should not be much of an issue in body mass estimation for fossil hominins, unless their mode of bipedalism differed significantly from locomotion of modern humans.

Konigsberg et al. (1998) and Hens et al. (2000) used calibration techniques for estimating stature in fossil hominins. Ordinary Least Squares (OLS) regression fits a line that minimizes the sum of squares of the vertical distance of each data point from the line. Because the relationship of these variables is linear the relationship is expressed as

$$y = a + bx + e \tag{2.1}$$

where y represents the unknown or dependent (response) variable, a is the intercept, b is the slope of the regression line, and e is the random error. The independent variable (x) is prone to measurement error and is often just a proxy for the actual variable of interest, so this procedure ("classical calibration") tends to introduce a systematic bias into estimates (Aykroyd et al., 1997), unless the means for the reference sample and target sample are similar (Konigsberg et al., 1998).

In the context of body mass estimation, "inverse calibration" is the multiple regression of body mass onto measures of "organ size" (such as tooth areas or measures of bone size). This is referred to as inverse calibration because it regresses global size (body mass) onto measures of local size (organ size), so the dependency of organ size on body mass is reversed in this model; this is in contrast to classical calibration, in which organ sizes are regressed onto body mass and these regressions are solved for body mass. In this study, the profile likelihood is also calculated for fossil specimens with more than one available measurement. Profile likelihood is "not a likelihood, but a likelihood maximized over nuisance parameters given the values of the parameters of interest" (Aitkin, 2005, p. 1). When inverse calibration is not favored (based on the R statistic), the profile likelihood estimator is preferred over the classical calibration estimator. In univariate analyses there is no profile likelihood estimator.

To test for individual deviations in size from a reference sample Brown (1993) suggested the quantity

$$R_x = (\hat{y} - \breve{y})'\Theta(\hat{y} - \breve{y}) \tag{2.2}$$

where $\hat{y}$ is a vector of bone measurements predicted by classical calibration to estimate body mass and the regression of bone measurements on body mass to predict bone measurements, $\breve{y}$ is a vector of bone measurements estimated by regressing body mass on bone measurements to estimate body mass and then regressing bone measurements on body mass to estimate observed bone measurements, and Θ is the inverse of the prediction variance covariance matrix (Konigsberg et al., 1998). R_x is asymptotically distributed as

a chi-square with one degree of freedom. The value of R_x reflects the difference between the target's body mass and the mean body mass from the reference sample (large values of R_x indicate large departure from the mean body mass). The R statistic measures allometric differences and is calculated as

$$R = (y_0 - \hat{y})'\Theta(y_0 - \hat{y}) \tag{2.3}$$

(Brown and Sundberg, 1987; Brown, 1993) where y_0 is a vector of observed bone measurements and $\hat{y}$ and Θ are as in the calculation of R_x (Konigsberg et al., 1998). R is asymptotically distributed as a chi-square with *q–1* degrees of freedom where q represents the number of bone measurements. In each case, departure from the reference mean is judged as significant when $\alpha < 0.05$.

In order to have general utility, any parametric statistical method for estimation or hypothesis testing should be recoverable from the appropriate summary statistics (Konigsberg, 1991; Konigsberg et al., 1998). This stricture makes it possible to apply methods without having recourse to the original raw data, and it makes it possible to "tailor make" estimators and tests in the light of missing data from new specimens. It also underscores the necessity for publishing the appropriate summary statistics. The reference sample (n = 568) has a variance-covariance matrix **V** on n-1 degrees of freedom and a vector of means for the log body weight and log bone measurements. There is no missing data in the reference sample.

Inverse calibration (regression of body mass on bone measurement) will give an unbiased estimate for specimens that do not differ significantly from the reference sample. In cases that require extrapolation, classical calibration (regression of bone measurement on body mass followed by solving for body mass) provides an unbiased estimate of body mass (Konigsberg et al., 1998).

Following previous work (Konigsberg et al., 1998; Hens et al., 2000) allometric differences are suspected between modern humans and at least some of the fossil hominins. If testing confirms this then profile likelihood is the most appropriate estimation technique. The multivariate classical calibration estimator is

$$x^i = (y_i - a)'C^{-1}b(bC^{-1}b)^{-1} \tag{2.4}$$

for each individual (i) where y is a vector of bone measurements, b is a vector of regression coefficients for bone measurements on body mass for the reference sample, a is a vector of y-intercepts for each measurement, and **C** is the variance-covariance matrix among bone measurements after removing the effect of body mass (Konigsberg et al., 1998).

2.2 Estimating Hominin Brain Size

A large relative brain size characterizes humans and, presumably, our most recent ancestors. Studying this relationship in modern humans is straightforward because we have bodies and brains available, but the question remains: at what point in our ancestry did hominin brain size begin to outpace increasing body mass? Endocranial volume (EV) estimates are the most common proxy for brain size. Values for fossil hominins usually come from previous research without a critical assessment of the estimation method used, without consideration of measurement error, and often without mention of how estimates were obtained. Accepted measures of EV that are currently used come from research by only a small number of anthropologists (Tobias, 1967; Holloway, 1970, 1980; Brown et al., 1993; Conroy et al., 1998; Falk et al., 2000), regardless of which fossil hominin is under consideration. The problems with EV estimates are closely tied to the salient problems in all analyses of fossils: sample size is too small and probably biased with regard to time period, sex, and geography, and many of the samples we do have are very fragmentary.

New research usually does not consider how these estimates were made because these EVs are often taken as correct following any kind of publication, including book chapters, which are not usually subject to rigorous peer review. Referring back to the original research reveals that final estimates are usually averages of multiple volumetric measurements of the same endocast, either from water displacement, mustard seed, or metal shot. Hawks (2011) illustrates the importance of point estimate choice. He uses a previously published value of 390ml for an incomplete specimen (KNM-WT 17400). This estimate of 390ml appears to have essentially been visually estimated (not measured) by Holloway (1988) and reaffirmed without explanation by Falk et al. (2000). Employing the Hubert test, he found no significant trend using the 390ml estimate for this specimen. However, Elton et al. (2001) employ the Hubert test for the same *P. boisei* specimen, but use a much larger estimate of 500ml proposed by Brown et al. (1993). Their results are significant (i.e., reject the null hypothesis of no trend) using this estimate.

Fossil hominin brain size estimation poses a number of challenges, so although fossil hominin's brain size estimates are widely published they are often hotly contested (e.g., Holloway, 1983; Falk, 1985). Tobias (1971) included all available estimates, as well as details of the controversies and lack of consensus over some specimens' estimates. Many of these estimates are made visually, by endocast reconstruction, or from a combination of cranial interlandmark distances and vault thickness measurements. The juvenility of many hominin specimens further complicates endocranial volume (EV) estimates because their juvenile EV estimates are often "adjusted" to adult capacities. I will address these adjustments shortly.

Regardless of the continued discovery of fossil hominin remains, the problems with endocranial volume estimates remain largely the same. Most remains are very fragmentary and some have questionable tax-

onomic affiliation. Sexual dimorphism also presents a challenge—do size differences represent males and females or different species? Quibbling about taxonomy can make discussions of means and trends difficult. For this reason it is sometimes necessary to be more general about taxonomy (i.e., only assigning a genus); taxonomy is less important than dating for a review of brain size over time.

Even ignoring issues of taxonomy and classification, there is a lack of consensus on the proper method for reconstruction of crania and/or endocasts, and endocranial volume estimation. Available methods include eyeballing it, measurement of reconstructed endocasts by water displacement, comparisons to more complete specimens that are measured directly, filling the cranial cavity with small objects (e.g., seeds, shot) and measuring their volume, relying on previous estimates, or, most recently, virtual endocasts produced and measured via CT scan.

Dart first described the Taung Child, the type specimen for *Australopithecus africanus* (Dart and Salmons, 1925), but did not offer an estimate of cranial capacity despite a well-preserved partial endocast. Sir Arthur Keith (1925) used a plasticine model of the endocast to estimate a cranial capacity of 450cc, but later estimates put it closer to a range of 500cc to 520cc (Zuckerman, 1928; Dart, 1926, 1929; Clark, 1947; Clark and Campbell, 1978). The adult estimate hinges on two parameters: the actual EV estimate and the age estimate of the Taung Child. Keith (1925) stated that a 4 year-old human has reached 81% of its brain size and used his 450cc estimate to arrive at an adult estimate of about 520cc. Dart (1926) added 20% to the 520cc estimate to arrive at an adult estimate of 625cc. Tobias (1965) used an updated comparative method based on hominoid dental development and used the juvenile estimate of 520cc to estimate Taung's would-be adult EV as 540cc. The existing literature on this well-studied skull contains a range of juvenile EV estimates from 404cc to 520cc (Falk, 1987), and adult estimates from 412cc to 728cc (De Miguel and Henneberg, 2001). Falk and Clarke (2007) reevaluated the Taung endocast with CT reconstruction and estimated smaller EVs than previous authors; the estimated actual (juvenile) EV is 382cc, with a projected adult capacity of 406cc.

Most estimated upper limits of both the juvenile and adult values for the Taung Child are larger than for preserved adult *Australopithecus africanus* specimens. Cranial capacities are estimated for 15 *Australopithecus africanus* specimens, ranging from 350cc-375cc (Sts 25, Wolpoff (1996)) to 650cc (MLD 1, Dart (1956)). Several issues could contribute to this large range; first, older EV estimates (e.g., Dart, 1956) were "eyeballed" and may be inaccurate, and second, there is probably sexual dimorphism in this species so females with smaller bodies would have smaller absolute brains (Broom, 1938).

Recently, Neubauer et al. (2012) have used CT scans and simulations to examine the effect of 'missing data uncertainty' (i.e., reconstructing incomplete specimens) and small sample size uncertainty on EV estimates

in *A. africanus*. Their four simulations include the use of chimpanzees as a reference sample, the problem of missing data, small sample size, and the "*A. africanus* situation," which combines the previous three situations. Their results compare estimates based on a chimpanzee reference sample to estimates based on the most complete *A. africanus* specimen (Sts 5) and suggest that chimpanzees form an acceptable reference sample for estimating EV while a human reference sample tends to cause overestimation. Their simulation approach is an important contribution to the continued study of endocranial volume.

Only four *Australopithecus afarensis* specimens exist for estimating cranial capacity; estimates range from 350cc (Falk, 1985) to 550cc (Kimbel et al., 2004). These specimens come from four formations in the Afar depression of eastern Africa, most notably from the Hadar site, which has yielded more than 90% of nearly 400 specimens (Kimbel et al., 2004). The dates (3.2 mya to 2.95 mya) for *Australopithecus afarensis* are narrow and distinctly bounded (Kimbel et al., 2004).

There is generally agreement as to the volume of *Australopithecus afarensis* brains, although there has been some controversy over the organization of the brain, particularly whether parietal and occipital reorganization pre- or post-dates brain enlargement (Holloway, 1983; Falk, 1985; Holloway, 1986; Falk, 1987). The juvenility of one of the four *A. afarensis* skulls (AL 333-105) also raises some questions. While the most complete adult skull (AL 444-2) has an estimated EV of ca. 550ml (Kimbel et al., 2004), the adult estimates for AL 333-105 are much lower, ranging from 340ml to ca. 400ml (Falk, 1985; Holloway, 1983). Holloway and Yuan (2004) argue that the large overall size and late temporal position of AL 444-2 accounts for the *A. africanus* EV discrepancy. Based on morphological similarities, Kimbel et al. (1994) argue for nearly a million years of stasis in this species.

Recently, White et al. (2009) described the remains of *Ardipithecus ramidus*, the purported ancestor of *Australopithecus afarensis*. More than 100 specimens represent *Ardipithecus ramidus* but there is only one cranium complete enough to allow reconstruction of cranial capacity through CT scan. The 300-350cc estimate (Suwa et al., 2009) is similar to the estimates for the much earlier *Sahelanthropus tchadensis*, which is estimated at 360-370cc (Zollikofer et al., 2005). Other morphological aspects (e.g., teeth) of *Ardipithecus ramidus* exhibit less variation (lower standard deviations) than *Australopithecus afarensis*.

The earliest *Homo* specimens from which EV is estimated date to about 1.9 mya, although earlier specimens attributed to *Homo* (e.g., A.L. 666-1 maxilla) date to about 2.33 mya (Kimbel et al., 1997). Although there is much debate about the origin and taxonomy of early *Homo*, the chronology of individual specimens is most important for the purposes of this research. Endocranial volume estimates for *Homo habilis* specimens mostly range from about 475cc to nearly 600cc (De Miguel and Henneberg, 2001), although a couple of estimates are as high as 750cc (Stringer, 1986). The higher estimates not only seem anomalous,

they are also the specimens for which measurement was most subjective (i.e., they were highly fragmentary and/or needed extensive reconstruction) (Holloway, 1973; Stringer, 1986).

For multiple reasons, research on the evolution of the relationship between hominin brain size and body mass has focused on Pleistocene *Homo* species. First, there are more and better preserved specimens, which provide more accurate estimates of both brain size and body mass through larger sample sizes and less reconstruction of specimens. Additionally, it is generally assumed that the large changes in brain size relative to body mass first appear in mid-Pleistocene *Homo erectus sensu lato* (Rightmire, 1981; Antón, 2003), so interest is naturally focused on that time period and species.

Homo erectus sensu lato includes both *Homo erectus* (*Homo erectus* found in Africa) and *Homo erectus sensu stricto* (*Homo erectus* found outside of Africa). Again, questions of taxonomy are less important for this research than dates. Currently, the earliest *Homo erectus* cranial remains have been found in Koobi Fora, represented by KNM-ER 3733 and dating to about 1.8 mya (Feibel et al., 1989). This specimen has several EV estimates, all ranging from 800cc–850cc (De Miguel and Henneberg, 2001). *Homo erectus* persisted in East Africa from 1.8 mya to about 780 ka , and may have concurrently occupied Swartkrans in South Africa (until ca. 1.0 mya), although the taxonomy of these specimens is still unclear (Antón, 2003).

Homo erectus was the first hominin to leave Africa and is found in Indonesia as early as 1.8 mya, persisting until less than 100 ka (Antón, 2003). Early Indonesian specimens include the partial crania of Sangiran 4, 27, 31, as well as the Perning skull. Sangiran 4 and 31 are among the earliest *Homo* specimens found outside of Africa. They date to $>$ 1.6Ma (Antón and Swisher III, 2004). Endocranial estimates for these specimens are 908cc (Sangiran 4) (Antón, 2002) and 1000cc (De Miguel and Henneberg, 2001). More recent Indonesian *Homo erectus* specimens Sangiran 2, 10, 12, 9, and 17 all date between 0.9 –1.4Ma (Antón, 2003) with estimated endocranial volumes of 850cc to 900cc (De Miguel and Henneberg, 2001). At less than 100 ka (Antón, 2003), specimens from Ngandong (1, 5, 6, 9, 10) and Sambungmacan (1, 3, 4) are found in Indonesia. Their endocranial volumes range from 900cc to 1316cc (see Table 3.6).

Homo erectus sensu lato specimens were found in Dmanisi, Republic of Georgia; these date to about 1.7 mya. The first two skulls from this site yielded EVs of 775cc (specimen D2280) and 650cc (specimen D2282) (Gabunia et al., 2000). An additional, remarkably well-preserved cranium, D2700, measures about 600cc in volume. There is currently no evidence of persistence of *Homo erectus* in Georgia.

Chinese deposits dating to about 1.2Ma contain *Homo erectus* cranial remains; the earliest cranial remains come from Gongwangling (Antón, 2003). This individual has an endocranial capacity of 780cc (De Miguel and Henneberg, 2001). The sites of Zhoukoudian, Nanjing, and Hexian have yielded crania from ca. 200 to 600 ka with endocranial volumes ranging from 855cc to $>$ 1200cc (Antón, 2003) (see Table 3.6).

Most analyses have focused on *Homo erectus* because of the larger and more complete sample compared to Australopithecines, as well as an assumed similarity to modern humans in body mass and proportion. *Homo erectus* remains show only slight fluctuations in endocranial volume over time, indicating an overall pattern of stasis, not a steady progression of larger cranial capacity (Rightmire, 1981; Leigh, 1992a). Rightmire (1981) posits that skulls and teeth of *Homo erectus* were mostly static, so rapid evolution must have been a hallmark of early *Homo sapiens* in the terminal Pleistocene. However, Rightmire (1981) did not test or correct for allometric differences (i.e., sexual dimorphism or evolutionary allometry). He and others with similar results (Henneberg, 1987) used some questionable EV estimates, had limited computing power and used OLS regression to detect a trend over time without accounting for autocorrelation.

Table 2.2: Body Mass and Cranial Capacity Estimates from Ruff et al. (1997)

Sample	Temporal range (ka)	Body mass (kg) mean ± s.e. (n)	Cranial capacity (cc) mean ± s.e. (n)
Living worldwide	—	58.2±1.0 (51)	1,349
Pecos Pueblo (29)	—	55.5±1.2	1,308±23 (29)
Late Upper Paleolithic	10-21	62.0±0.9 (71)	1,466±35 (23)
Early Upper Paleolithic	21-35	66.6±1.3 (33)	1,517±30 (15)
Late archaic *Homo sapiens*	36-75	76.0±1.4 (17)	1,498±45 (14)
Skhul-Qafzeh	90	66.6±2.2 (10)	1,502±45 (6)
early Late Pleistocene	100-150	67.7±2.4 (10)	1,354±41(8)
late Middle Pleistocene	200-300	65.6±5.1(6)	1,186 ±32 (17)
middle Middle Pleistocene	400-550	67.9±6.4 (5)	1,090±38 (12)
late Early to early Middle Pleistocene	600-1,150	58.0±4.3 (3)	856±52 (7)
Early Pleistocene	1,200-1,800	61.8±4.0 (5)	914±45 (5)

2.3 Overcoming Statistical Challenges

Even with several, well-preserved fossil specimens, the construction of a reference sample is still of concern. This study uses a modern human reference sample comprised of measurements following McHenry (1992a) and Buikstra et al. (1994). The rationale for these measurements is two-fold. First, the measurements from each are widely used for fossil material (e.g., Leakey et al., 1995; Lordkipanidze et al., 2007; Ruff, 2002; Márquez et al., 2001; Carretero et al., 1997). A reference sample is of limited use if it does not contain the measurements analogous to those of fossils. Second, these measurements include joint surfaces and lengths and widths of long bones—aspects of the skeleton previously identified as useful for body mass estimation Auerbach and Ruff (e.g., 2004).

There is no way around using extant species as reference samples for extinct species, but early studies did

not consider the implication of the reference sample choice. Many just used any human skeletal material they had. As computing and statistical power has increased, the importance of reference sample structure has come to the forefront. Jungers (1985) has advocated only using hominoids as references for fossil hominids. Konigsberg et al. (1998) propose a model, stemming from Brown (1993) and Brown and Sundberg (1987), for estimating both allometric and size differences between a target and the reference sample, which is informative when the species comprising the reference sample differ from the target specimen.

As described above, the R and R_x statistics give a measure of difference in size and allometry of the target specimen from the reference sample. The construction of a regression model is another issue in itself. Many bivariate methods exist (e.g., using femoral head) (Grine et al., 1995; Ruff et al., 1997), but a common assumption is that more information is desirable. Smith (2002) discusses whether one should construct a multiple regression equation or just use a series of bivariate equations and average estimates. The former is preferable because it accounts for multicollinearity of variables and makes the construction of confidence intervals straightforward. Statistically, it is not clear how one would combine several point estimates, each with different measures of uncertainty (confidence intervals or standard errors). If one variable is clearly superior to all others it is also valid to just use one bivariate model—the inclusion of additional information just for the sake of more information may not improve the model.

Body mass is most often estimated through the use of linear regression and the association of certain skeletal measurements with living size. Analysis of modern human skeletal material generally makes use of long bone lengths to assess stature; articular surfaces or diaphyseal measurements are preferred for body mass estimation. Many studies use articular surfaces because of the scarcity of complete long bones in the fossil record. Regardless of which skeletal element is used, issues with estimating body mass for fossil hominids persist. Generally the reference (known) sample for these estimates consists of modern humans and/or other extant primates, but many fossil hominins have body proportions that differ from both of these groups (Konigsberg et al., 1998). Except in cases where most of the fossil is present and can be directly measured, as with KNM-WT 15000 (Walker and Leakey, 1993), body mass estimates are based on reference samples that may be less than ideal.

Konigsberg et al. (1998) and Hens et al. (2000) also explore the use of different regression techniques and their ability to estimate stature for fossil hominins. This can (presumably) be extended to the very similar endeavor of body mass estimation. Both studies use relatively complete fossil hominins (A.L. 288-1 in both analyses, and Hens et al. [2000] also include KNM-WT 15000) as test cases for their methods. Five estimation techniques are employed: two ordinary least squares regressions (inverse and classical calibration), major axis regression, reduced major axis regression and a femur/stature ratio. The femur/stature ratio

was developed on modern humans (Feldesman and Lundy, 1988; Lundy and Feldesman, 1989); it assumes isometry because it uses a constant ratio. Fossil hominins hind limbs scale differently than modern humans (Jungers, 1982, 1984) so the femur/stature ratio does not work well in that context. Major axis and reduced major axis regression have been strongly suggested (Raynor, 1985, Aiello, 1992) because they assume error in measurement of both the dependent and independent variables. These differ from ordinary least square regression because the errors are calculated perpendicular to the best fit line rather than vertically. In reduced major axis the variables are standardized by their standard deviations. However, Konigsberg et al. (1998) and Hens et al. (2000) found that for fossil hominins classical calibration provides the best estimate of stature. The inverse estimator is the typical ordinary least squares regression where stature is the dependent variable. Classical calibration regresses the skeletal measurement on stature and then solves for stature. Although the risks of extrapolating are well-known (Smith, 2002), it is often unavoidable in the case of fossil hominins. The use of classical calibration and calculation of the R and Rx statistics can inform responsible estimates for fossil hominin body mass.

Konigsberg et al. (1998) noted that the inverse calibration estimator is a Bayesian estimator, while classical calibration is a maximum likelihood estimator. While the former statement is correct, the latter is only correct under certain conditions described in Brown and Sundberg (1989). Specifically, if only a single measure of organ size is used to estimate body mass in classical calibration, then classical calibration gives the maximum likelihood estimate (this is the case for fossil specimens with only one available postcranial measurement). Another condition under which classical calibration becomes the maximum likelihood estimator is as the reference sample size becomes quite large. Konigsberg et al. (1998) did not discuss or present the profile likelihood method extensively covered in Brown and Sundberg (1987; 1989) and Brown (1993), but the profile likelihood method does provide the maximum likelihood estimate (Brown and Sundberg, 1987; Brown, 1993).

Inverse calibration is inherently Bayesian (Uhl et al., 2013) and relies on the reference sample as an informative prior. In this case, the reference sample is comprised of modern humans but the dependent variable is the body mass of a fossil hominin. An accurate estimation is possible only if the chosen skeletal variables (e.g., femoral head diameter, femoral midshaft diameter) have the same relationship to body mass in fossil hominins as they do in modern humans. Given documented allometric differences in extant, closely-related species (Hartwig-Scherer and Martin, 1992), this is a questionable assumption, but Brown (1993) introduced a method for testing and quantifying deviation in size or allometry of an individual from the reference sample. In this context the deviation of a fossil hominin specimen from the reference sample of modern humans is tested and quantified.

Smith (2002) critiqued almost every aspect of body mass estimation from a statistical standpoint. While his analysis of the state of body mass estimation is rightly critical, some limitations of fossil hominin data cannot be completely overcome. Sample size, although it grows over time, will always be an issue; phylogenies will never be agreed upon; reference samples will always consist of species different from those being estimated. Because of these issues, estimates of body mass will always carry a measure of uncertainty. Honesty about these limitations is critical. Estimates of body mass should always be accompanied by measures of uncertainty like confidence intervals or the standard errors of the estimates. Estimating from estimates should be limited—the use of a stature estimate to estimate body mass only compounds the uncertainty in each estimate. The level of uncertainty of an estimate can be informed by calculated differences between the target and reference sample (R and R_x) statistics and studies on relatively complete fossil specimens.

2.4 Hominin Brain Size and Body Mass Evolution

2.4.1 Brain Size Allometry

Allometric relationships between brain size and body mass have been calculated for over a century (e.g., Huxley, 1924); the steps to calculate these relationships form the crux of the main research questions addressed by this research. Jerison (1973) synthesized much data on this relationship and found that most mammals have brains that scale to the $\frac{2}{3}$ power of body weight (Pilbeam and Gould, 1974). A reconsideration of larger data samples including a diverse array of mammals suggests that that scaling power may instead be $\frac{3}{4}$ (Martin, 1981; Hofman, 1983). The scaling power from the larger data set is generally accepted, but what is more striking than the actual number is that the scaling power stays relatively constant for most mammals. Pilbeam and Gould (1974) point out that a scaling power of $\frac{2}{3}$ would add just enough neural tissue to neurologically control the additional body mass. The authors define "encephalization" as any scaling relationship of brain size to body mass that exceeds 0.66. Their scaling estimate in a *Homo* lineage is 1.73. This estimate is not without problems, but demonstrates that significant brain and body changes have happened in humans compared to other mammals and primates. Isometry (1.0) would indicate that brain size increase has been purely a consequence of body mass increase or *vice versa*. The $\frac{3}{4}$ scaling value indicates that brains do not seem to "keep up" with bodies in most mammal species (negative allometry); however, modern human brains and at least some fossil hominin brains have clearly outpaced increasingly large bodies.

Jerison(1973) covers brain evolution from invertebrates all the way through primates and hominins. Much

of the early work on brain:body size relationships was merely quantitative and broadly adaptationist. There was not much critical thought about big brains other than that a big brain must be a good thing. Jerison explores reasons that big brains would confer a selective advantage; he cites common reasons including language, sociality, hunting and home ranges. These reasons were inconsistent with the view of human brain evolution at this time because other mammals exhibited the same traits without such a large increase in brain size (e.g., wolves hunting in packs) and the parts of the brain that control language and sociality are relatively small compared to overall brain size. Enhancing those characteristics or brain regions would not necessarily require an overall increase in brain size.

The studies of Jerison (1973), Pilbeam and Gould (1974), and Martin (1981) all point out an important consideration that differences exist in scaling values for inter- *versus* intraspecies analyses. Bookstein et al. (1978) discusses these as a statistical artifact of the scale at which one is choosing to look at scaling relationships. Cheverud (1982) defines three types of allometry. Allometric differences can occur within an individual during ontogeny (ontogenetic allometry), between two individuals (e.g., a male and a female) within a species (static allometry), or between species during evolution (evolutionary allometry). Ontogenetic allometry, such as that experimentally produced in mice, underlies static and evolutionary allometry. Humans have overcome constraint to grow relatively large brains, probably through a decrease in genetic covariation of brain and body growth. It is currently unknown at what point in our ancestry hominin brain growth exceeded body growth. Evolutionary allometry can arise as an adaptation via an optimized functional relationship between two traits, or as a result of constraints of static (within-species) allometry (Hansen and Bartoszek, 2012).

Although hominin species are closely related, they likely scale differently in multiple ways: postcranial measurements scale differently to overall body mass, and brain size scales differently to body mass. Both of these allometric relationships are of interest here. Allometric differences between a reference sample and a target specimen can require extrapolation, thus precluding confidence in body mass estimates made by inverse calibration (regression of body mass on bone measurement). Konigsberg et al. (1998) applied the R statistic (a measurement of allometric difference between a reference sample and target specimen) to the estimation of stature using long bones (Brown and Sundberg, 1987). When R is significant it indicates that the target specimen scales differently than the reference sample (Konigsberg et al., 1998). Tackling this problem is informed by quantitative genetics and the employment of theories about phenotypic integration. All organisms are collections of integrated traits resulting from genetic covariance. Species differ in their patterns of integration, which changes the relationship of traits (i.e., the way overall body mass scales to individual bone size and the way brain size scales to body mass).

A poor understanding of the genetics and mechanisms of evolution have led many to believe that phenotypic change is 1. always an adaptation and, 2. happening in isolation from the rest of the phenome. Before Lande's (1979) application of quantitative genetic methods many assumed that allometric changes were merely the consequence of selection on body mass and the correlated response of brain size. His work indicates that this is probably the case for mice, in whom brain size is largely a correlated response to directional selection on body mass. When brain size and body mass are highly positively correlated then a change in one of the traits produces a correlated response in the other. Encephalization would require either antagonistic selection (selection for larger brains and smaller bodies) or would result in gigantism. However, according to Lande (1979), over the course of primate evolution the genetic correlation of brain size and body mass has decreased significantly. Thus, some primates have become encephalized because of the low genetic correlation between brain size and body mass and either directional selection or random genetic drift resulting in larger brains.

Following directly from Lande (1979), a series of experiments on randombred mice suggests that the progression of ontogeny may underlie much of the evolutionary variation in the brain size/body mass relationship (Atchley et al., 1984; Riska and Atchley, 1985). First, Atchley (1984) tested the effect of direct selection for body size on brain size in rats. Rats selected for large body size had correlated increases in brain size, although brains did not increase isometrically with bodies. Interestingly, there were sex differences in divergence from control lines; males responded more to selection for large body size but ended up with smaller brains per unit of body weight than females. One control line experienced a statistically significant divergence in brain size increase compared to other controls; the author attributes this to genetic drift. The down-selected rats diverged from the controls in terms of body size but not brain size, indicating there may be a minimum physiological size that the brain must maintain. The rats were also selected for rate of development, but this selection did not cause divergence in brain size as did the selection on body size. These results are indicative of a high correlation of brain size (growth) with body size (growth) (Atchley, 1984).

Early in ontogeny brains and bodies are both growing by many of the same processes, producing a high correlation between the two variables. However, in humans, adult brain size is reached (i.e., the brain stops growing) long before adult body mass is reached, thus significantly reducing the correlation of the two variables. Between-species changes in the timing of this reduced correlation (presumably because of differential selection) could quickly produce evolutionary variation in the brain size/body mass relationship. In mice, brain size is more heritable than body size (additive genetic variance > 0.6 for brain size across 70 days of ontogeny, additive genetic variance $= 0.25$ at 38 days and 0.21 at 70 days for body size) (Atchley

et al., 1984). The genetic correlation of brain size and body size in mice is large and positive between birth and 14 days. It is smaller but still positive between 14 and 21 days, but becomes large and negative between 21 and 38 days. The authors note that the average inflection point for the Gompertz growth curves fitted to body weight is around 21 days (20 and 22 for females and males, respectively). While studies of mice and rats relay important empirical evidence not available for humans, it is apparent that different patterns of covariance and development manifest in humans.

In the ensuing decades anthropologists and developmental biologists have learned much more about the underlying genetic and hormonal mechanisms (e.g., Leigh and Shea, 1996; Leigh, 2001; Müller, 2007; Rolian, 2009). In all mammals, particularly humans, this has proved to be a composite of tightly regulated genetic controls, genetic-mediated chemical interactions, and environmental (including *in utero*) effects, each in different combinations based on body part/region and developmental stage and subject to change via drift or selection. The story of hominin brain evolution is complex, requiring consideration of many factors: adaptive and non-adaptive biological processes, ontogeny, species differences, theoretical and methodological framework and dataset construction. The general consensus remains only that the hominin lineage has experienced a large increase (and slight recent decrease) in relative brain size during the course of our evolution. Whether this resulted from directional selection or genetic drift, punctuated equilibrium or gradualism, and if and how it correlates with body mass, dietary, metabolic and climate changes all remain fruitful grounds for continuing research.

Much of the older literature uses OLS regression (cranial capacity or some other morphological metric trait regressed on time) to analyze temporal trends in brain size (Lestrel and Read, 1973; Lestrel, 1976; Rightmire, 1981, 1986, e.g.,), but these methods are inappropriate for many reasons, even when the data is log transformed (Godfrey and Jacobs, 1981). First, data that come from points in time are almost surely autocorrelated. The cranial capacity of a hominin at one point in time is not independent from the cranial capacity of the hominins that came before it in the time sequence (Leigh, 1992). Lee and Wolpoff (2003) also point out that regression is inappropriate because it merely tests whether the slope of the regression line is different from zero. However, the question is not whether the brain expanded during hominin evolution (it surely did), but how it changed. OLS regression is not suited for analysis of such a trend, although it is employed in body mass estimation in this research.

Despite the obvious cranial change in the *Homo* lineage, authors cannot agree as to the underlying evolutionary mechanism. Most of the debate centers on the rate of evolution (punctuated equilibrium [(Eldredge and Gould, 1972; Rightmire, 1981; Leigh, 1992b)] versus gradualism [(Wolpoff, 1984, 1986; Lee and Wolpoff, 2003)]), the mode of evolution (e.g., genetic drift, directional selection), and the timing (e.g.,

the role of heterochrony). As an alternative to gradualism, punctuated equilibrium (Gould and Eldredge, 1977) posits that most species experience long periods of time with little morphological change that is punctuated by short periods of rapid change. Some have suggested that early *Homo* experienced one of these punctuated time periods, especially with regard to encephalization (Hofman, 1983).

Leigh (1992) applied a times series method, the Hubert test (Konigsberg, 1990), to look for trends in cranial capacity in Pleistocene hominins. Leigh's (1992) conclusions contradict some earlier studies as he found a significant positive trend in increasing cranial capacity in *Homo erectus* specimens. The non-parametric Hubert test is preferred over other types of regression (including Major Axis and Reduced Major Axis) because it minimizes error from unequal time intervals. Error in time interval data comes from two sources: first there is measurement error and inherent estimation error associated with dating techniques, which is why properly constructed dates for fossil hominins consist of ranges rather than point estimates. Second, because of the almost random nature of fossil hominid discoveries, time intervals between documented and dated fossils are uneven. The Hubert test orders data from earliest to latest so it does not assume a constant interval length between data points and it also allows multiple observations for the same geological age (Leigh, 1992).

Contrary to Leigh (1992), Ruff et al. (1997) found stasis in relative brain size in *Homo* between 1.8 mya and 600 ka. A decrease in cranial volume has been widely documented in the terminal Pleistocene or early Holocene. The decrease in cranial capacity could be biologically related to reorganization of the brain (Holloway, 1967), a period of stasis between punctuated events (Henneberg, 1988), selection for smaller body mass, climatic variation, and/or thermoregulatory mechanisms either directly related to brain function or secondary to changes in body mass and/or proportions (Beals et al., 1984). Hawks (2011) tested whether a recent decrease in body mass is a sufficient explanation for the corresponding decrease in brain size and, consistent with Lande (1979), found that the decrease in brain size is not merely an allometric consequence of changes in body mass. He offers several adaptive and non-adaptive hypotheses for future testing, including genetic drift, plasticity, development and brain reorganization.

Pagel's (2002) modelling method uses multiple scaling parameters to establish a phylogeny and the relatedness of those species in the tree based on a morphological trait and scaled to relatedness. The parameters affect the values of the variance-covariance matrix. The phylogeny scaling parameter (λ) is a scalar that estimates the role of the phylogeny in trait similarity. If λ is 0, all of the similarity is assumed independent of phylogeny. The path scaling parameter (δ) is a power to which components of the variance-covariance matrix are raised. It gives a sense of evolutionary rate because it scales the path from a root to a terminus; any value different than 1 implies either accelerating or decelerating gradualism in the trait. The

final parameter scales the branch length and is depicted by κ. At a value of 1, κ indicates that evolution is proportional to branch length, which supposes gradualism. A value for κ greater than 1 could be consistent with a punctuated pattern.

A directional model, as opposed to a random-walk or unscaled-directional model, provides the best fit for Pagel's (2002) hominin cranial capacity data. He found evidence of both increasing cranial capacity over time and a recent acceleration of cranial capacity increase. There are some drawbacks to Pagel's analysis, including the need to assume a certain phylogeny is correct. This is an issue in all analyses of human evolution. With high-powered computing one could use Markov-Chain-Monte-Carlo (MCMC) methods to assess models for every possible phylogeny (Pagel, 2002).

Bookstein et al. (1978) argue that debates between punctuated equilibrium and gradualism create a false dichotomy and are overly simplistic for explaining something as complex as mammalian evolution and speciation. They show change in molar size of an Eocene primate (*Pelycodus*) over 1.2 mya. During that time period they identify six instances of gradualism (three increasing in size, three decreasing in size), one period of stasis, and one saltation.

2.4.2 Evolutionary Trade-Offs

While an increased brain size seems like it would give hominins a selective advantage, the evolutionary story is not so simple. Growing and maintaining a large brain requires tradeoffs in either life history, energy allocation, or both because nervous tissue is metabolically expensive. Theories about the mode of evolution driving increasing brain size revolve around directional selection for a host of reasons including anatomical changes (Aiello and Wheeler, 1995), sociality (Dunbar, 2009), cognition (Richerson and Boyd, 1999), hunting skills and dietary changes (Finarelli and Flynn, 2009), or climate change (Beals et al., 1984). Lande (1979) suggested that this kind of intense directional selection on brain size was possible because of a decoupling of genetic correlation of brain size and body mass. This is turn would have allowed both brain size and body mass to increase at the same time through directional selection on each. Brain size was possibly reined in by obstetric constraint imposed by pelvic rearrangement in bipedal hominins (Leutenegger and Cheverud, 1982; Rosenberg and Trevathan, 1995).

Probably most famously, Aiello and Wheeler (1995) posited that changes to the human brain were contemporaneous to changes to the human gut. To add something as energetically expensive as a very large brain without increasing basal metabolic rate (BMR) (Aiello and Wheeler, 1995), the human body had to undergo significant changes to its bauplan. To serve a bigger brain without increasing BMR would mean that energy expenditure was cut somewhere else. The heart and kidneys consume more energy than the

brain but are not larger than expected for a primate of our size. However, Aiello and Wheeler (1995) found that the only major organ that was smaller than was expected for a primate of our size (ca. 65 kg) was the gut.

A tradeoff with the gut could be two-fold: a smaller gut would use less energy, and it could be accompanied by an increased ability to extract nutrients and energy from food. Aiello and Wheeler (1995) state "that the relationship between relative brain size and diet is primarily a relationship between relative brain size and relative gut size, the latter being determined by dietary quality" (p. 207). While this statement was drawing mostly on others' data, subsequent empirical work has supported it (e.g., Fish and Lockwood, 2003). However, when gut area rather than gut mass is used, humans do not appear to be any more specialized than other primates. Hladik et al. (1999) argue that humans' carnivory (as a part of omnivory) is a specialization, but so are primate diets that are primarily frugivorous or folivorous.

"Man the Hunter" (Washburn, 1968) is an unlikely scenario for human evolution, rather early hominins were probably opportunistic scavengers. Speth (1989) contends that meat was only a marginal source of nutrition for scavenging hominins. His argument is based on several factors impacting humans' use of meat, including the inability to extract all the nutritional content from animal tissue, as well as the relatively low fat content of most African ungulates (what early hominins probably would have been scavenging). Additionally, he asserts that the vegetation available on the African savannah is fairly high protein—enough to supply most of the protein for hominins.

Another way that diet and relative brain size may be linked is through primate or hominins' increased abilities to create and retain spatial maps of resources (Aiello, 1997). This has been noted in many extant foraging primates (Milton, 1980; Harvey et al., 1980). There is a clear relationship between guts/diets and relative brain size, but one could argue that diet and spatial skills either primarily drove encephalization (selection pressure) or released constraint on brain size. Aiello (1997) notes that because brains *require* the extra nutrition and energy provided by a high quality diet and small gut they must have been drivers of brain size evolution. Leonard et al. (2007) support this and additionally argue that humans are"under muscled" and "overfat" compared to other primates. However, one cannot discount that there could be other factors, including sociality, life history, etc. contributing to encephalization.

Recently, Isler and van Schaik (2009) have formed the "Expensive Tissue Hypothesis." This is an attempt to take a broader, empirical look at brain size and its relationship to the body and life history in mammals and birds. They explain general trends, for example, "paying" for a larger brain requires either increased energy or a reallocation of available energy. The change in energy allocation can take many forms in mammals and birds. For example, flightless birds have larger relative brains because they do not have to maintain large

pectoral muscle for powered flight. Humans show an "under muscled" (Leonard et al., 2007) trend, as well as a small gut (Aiello and Wheeler, 1995). A change in energy allocation also effects growth and reproduction, in turn affecting life history. A decrease in overall growth would be expected with larger brains, as would decreased overall reproduction and increased interbirth intervals. The prediction of decreased overall growth is interesting in the context of humans, who have seemingly increased body size over the past 3-4 mya.

The energy requirement of a large brain also influences reproductive strategy. From an allocation perspective, one would assume that larger-brained species have fewer offspring who also have larger brains, requiring a larger investment on the mother's part. Isler and van Schaik (2009) confirm this across species. In monotokous, precocious mammals (including humans and other primates), development is slowed and fertility is reduced; a longer lifespan is compensation. In fossil hominins and modern humans, birthing large bodied and large brained offspring is also constrained by a pelvis modified for bipedal locomotion, probably requiring an even longer developmental period for offspring. Isler and van Schaik (2009) found behavioral modifications in polytokous carnivores (e.g., canids) that provide energetic support to gestating females and therefore reduce constraint on litter size. Reiches et al. (2009) note that humans differ from other primates in that we have, seemingly paradoxically, higher reproductive output but protracted juvenility. They give several reasons, mostly related to alloparenting, not in its usual context of increasing offspring survival, but its role in relaxing the energy demand on the mother. Through alloparenting, juveniles, other adult females, and adult males, can contribute to the energy requirements of the offspring, both during and after gestation.

Brain size is intrinsically tied to many other aspects of hominin biology and behavior. A better understanding of the rate and timing of brain size increase during human evolution (the goal of this research) will provide a framework for testing hypotheses about hominin biology, behavior, and ecology. The consequences and requirements for the modern human condition (large bodies and large brains), and thus, this research could contribute knowledge about important and poorly understood phenomena like the evolution of bipedalism, the life history and biology of other hominins (e.g., *Homo floresiensis*), human and non-human primate biology, behavior, and life history.

Although they have been raging for more than a century, arguments about the rate or mechanism of encephalization in fossil hominins and modern humans may be premature. The first steps in understanding human brain evolution are gaining a more accurate sense of the rate and timing of relative brain increases, and being honest about the limitations imposed by the availability of fossil hominin specimens. Only after resolution of these issues can we form testable hypotheses about the role of selection vs. drift, gradualism vs. punctuated equilibria and stasis, ecology, behavior, or growth.

Chapter 3

Materials and Methods

3.1 Materials

3.1.1 Skeletal Collections

Modern human skeletal measurements were taken on two cadaveric collections: the Pretoria Bone Collection, housed at the University of Pretoria, South Africa, and the Hamann-Todd Collection, housed at the Cleveland Museum of Natural History. These are all "known" individuals with recorded age, sex, stature and body mass. The Hamann-Todd Collection is composed of Americans of both European and African ancestry, most of whom died in the early 20th century. The Pretoria Bone Collection is an actively growing collection of South Africans of both European and African ancestry, all of whom have died since 1954. Measurements from individuals in these collections comprise the reference sample. The data set includes two repetitions of postcranial measurements modified from McHenry (1992) for each individual in the reference sample (Table 3.1). These measurements include maximum length of long bones of the limbs, as well as some measures of articular surfaces. Over 550 individuals (n = 568) comprise the sample and there is no missing data. Femoral head is traditionally used as an estimator of body mass, despite its low correlation with body mass (Uhl et al., 2013), but other measures (i.e., shaft diameter, orbital size) have also been used (Auerbach and Ruff, 2004; Kappelman, 1996).

Table 3.1: Reference Sample Postcranial Measurements

Measurement	**Description**	**Reference**
Humerus Maximum Length (HML)	Direct distance from the most superior point on the head of the humerus to the most inferior point on the trochlea	(Buikstra et al., 1994, p. 80)
Humeral Head Diameter (HHD)	Maximum anteroposterior diameter of the humeral head taken perpendicular to the shaft axis	(McHenry, 1992a, p. 408)
Humeral Maximum Diameter at Midshaft (HMSMax)	Maximum diameter at midshaft	(Buikstra et al., 1994, p. 80)
Humeral Minimum Diameter at Midshaft (HMSMin)	Minimum diameter at midshaft	(Buikstra et al., 1994, p.80)
Humeral Epicondylar Breadth (HECB)	Distance of the most laterally protruding point on the lateral epicondyle from the corresponding projection of the medial epicondyle	(Buikstra et al., 1994, p.80)
Capitulum Height (CapH)	Distance from the anteroproximal border of the capitulum to the distoposterior along the midline	(McHenry, 1992a, p. 408-409)
Humeral Articular Width (HAW)	The maximum width of the anterior aspect of the articular surface from the lateral border of the capitulum to the edge of the articular surface medially	(McHenry, 1992a, p. 409)

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Table 3.1 – continued from previous page

Measurement	Description	Reference
Radius Length (RML)	Distance from the most proximally positioned point on the head of the radius to the tip of the styloid process without regard for the long axis of the bone	(Buikstra et al., 1994, p. 80)
Radius Head Diameter (RHD)	Maximum width of the radial head	(Buikstra et al., 1994, p.80)
Ulna Maximum Length (UML)	Distance from the most superior point on the olecranon to the most inferior point on the styloid process	(Buikstra et al., 1994, p.81)
Femur Maximum Length (FML)	Distance from the most superior point on the head of the femur to the most inferior point on the distal condyles	(Buikstra et al., 1994, p. 82)
Femoral Head Diameter (FHD)	The maximum superioinferior diameter of the femoral head	(McHenry, 1992a, p. 409)
Femoral Anterior-Posterior Subtrochanteric Diameter (FAPST)	Distance between anterior and posterior surfaces at the proximal end of the diaphysis, measured perpendicular to the medial-lateral diameter	(Buikstra et al., 1994, p. 82)
Femoral Transverse Subtrochanteric Diameter (FTST)	Distance between the medial and lateral surfaces at the proximal end of the diaphysis, measured perpendicular to the anterior-posterior diameter	(Buikstra et al., 1994, p. 82)

Continued on next page

Table 3.1 – continued from previous page

Measurement	Description	Reference
Femoral Anterioposterior Midshaft Diameter (FAPMS)	Distance between anterior and posterior surfaces measured approximately at the midpoint of the diaphysis, and the highest elevation of the linea aspera	(Buikstra et al., 1994, p.83)
Femoral Transverse Midshaft Diameter (FTMS)	Distance between medial and lateral surfaces measured approximately at the midpoint of the diaphysis, and the highest elevation of the line aspera	(Buikstra et al., 1994, p.83)
Femoral Distal Anteroposterior Shaft Diameter (FDAPD)	The maximum anteroposterior diameter of the shaft at the distal end excluding the distal epiphysis	(McHenry and Corruccini, 1978, p. 476)
Femoral Distal Transverse Shaft Diameter (FDTD)	The maximum transverse diameter of the shaft at the distal end excluding the distal epiphysis	(McHenry and Corruccini, 1978, p.476)
Femoral Epicondylar Breadth (FECB)	Distance between the two most laterally projecting points on the epicondyles	(Buikstra et al., 1994, p. 82)
Tibial Maximum Length (TML)	Distance from the superior articular surface of the lateral condyle to the tip of the medial malleolus	(Buikstra et al., 1994, p. 83)

Both the Pretoria Bone Collection and the Hamann Todd Collection are cadaveric. Cadaveric body mass measurements can be problematic for multiple reasons. Obviously, the remains come from individuals who have died. Many causes of death can alter body mass, typically making it less upon death than it would be during life. Bodies can also lose mass as time passes from death to intake and measurement by the curators of the collection. Additionally, technicians can introduce measurement error through inconsistent or incorrect technique, transcription errors, or other mistakes. Data reliability issues (e.g., accuracy of recorded ages,

accuracy of living stature) plague most research using skeletal collections but there are limited amounts of known skeletal remains available, so they are often still used, but with caveats.

Todd's main concern with body weights from the Hamann-Todd Collection was overestimation.

> It is the weight of the emaciated body of chronic disease which we so persistently overestimated. So while the male White weight in Table 71! is 125.0 lbs. that in Table 71 is but 112.9 lbs. Our overestimates of these cadavera varied between about 15 and 25 lbs (Todd and Lindala, 1928, p. 28)

In this quote from Todd and Lindala, Table 71! contained the mean known body weights from 50 white males, while Table 71 contained the mean estimated weights from the same individuals. A systematic bias in this project's reference data could impact individual estimates in the same direction.

3.1.2 Hominin Fossil Postcranial Measurements

Postcranial measurements and endocranial volume (EV) estimates for fossil hominins have been culled from many literature sources (see Table 3.2 and Table 3.6). These measurements of fossil hominin individuals form the target samples. R and Rx statistics (described in detail below) were calculated for any fossil specimen with more than one postcranial measurement. Body mass is still predicted for those with only one postcranial measurement, but at least two measurements are required to discern a departure from the reference sample in size or allometry. De Miguel and Henneberg (2001) compiled estimates of EVs from the literature from about 3.2 mya to 10 ka, which included over 600 measurements for 243 hominins (see Table 3.6). Other measures of EV and dates for all fossil specimens (postcranial measurements and EVs) come from the literature. See Table 3.2 and Table 3.6 for specific sources. In some cases, numbers published as measurements of a fossil may be an estimate based on available measures of a specimen. The paleoanthropology literature can be surprisingly opaque about which features are measured directly versus estimated. I have made an effort to limit the inclusion of estimates, particularly those that seem most unfounded (e.g., estimating femoral head size from tarsal size), but the data set does still include some estimates. Most of these are measured directly, perhaps after reconstruction. The admittance of any estimate which will then be used as a basis for estimating body size increases the amount of error in the estimate.

Table 3.2: Fossil Postcranial Measurements

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
KNM-KP 271	*Australopithecus anamensis*	4.1 mya	HECB (60.2mm); CapH (19.4mm); HAW (44.8mm)	McHenry and Brown (2008); Bacon (2000)
Stw 431	*Australopithecus africanus*	4.0 mya	HECB (59.4mm); CapH (19mm); HAW (40.5mm)	Toussaint et al. (2003); McHenry and Brown (2008)
KSD-VP-1/1	*Australopithecus afarensis*	3.58 mya	TML (355mm)	Haile-Selassie et al. (2010)
MAK-VP-1/1	*Australopithecus afarensis*	3.4 mya	FAPST (21.2mm); FTST (29.5mm)	Lovejoy et al. (2002); White (2006)
MAK-VP-1/3	*Australopithecus afarensis*	3.4 mya	HML (296mm)	Kimbel et al. (1994)
AL 128-1	*Australopithecus afarensis*	3.4 mya	FAPST (19.2mm); FTST (28.9mm)	McHenry (1988)
AL 129-1b	*Australopithecus afarensis*	3.4 mya	FECB (56.5mm); FDAPD (21.1mm); FDTD (24.2mm)	Lovejoy et al. (1982a)
AL 137-48a	*Australopithecus afarensis*	3.1 mya	HECB (49.6mm); CAPH (14.64mm); HAW (36mm)	Reno et al. (2010); McHenry and Brown (2008)
AL 137-50	*Australopithecus afarensis*	3.4 mya	HML (295mm) FH (38.3mm)	Kimbel et al. (1994); Reno et al. (2010)
AL 152-2	*Australopithecus afarensis*	3.1 mya	FH (32.9mm); FAPST (16.9mm); FTST (23.5mm)	Ward et al. (2012)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
AL 211-1	*Australopithecus afarensis*	3.1 mya	FH (33.1mm); FAPST (16.9mm); FTST (23.5)	Lovejoy et al. (1982a)
AL 223-23	*Australopithecus afarensis*	3.1 mya	FH (35.3mm)	Reno et al. (2010)
AL 288-1 (Lucy)	*Australopithecus afarensis*	3.1 mya	HML (286mm); HHAP (26.8mm); HECB (41.1mm); CapH (12.3mm); HAW (30.1mm); RHD (15.1mm); FML (280mm); FH (28.6mm); FAPST (17.7mm); FTST (24.4mm); FAPMS (16mm); FECB (56.7mm); FDAPD (22.9m); FDTD (24.5mm); TML (233mm)	Johanson et al. (1982)
AL 322-1	*Australopithecus afarensis*	3.1 mya	HECB (45.7mm); CapH (15.4mm); HAW (34.1mm); FH (27.9mm)	Lovejoy et al. (1982b); Reno et al. (2010)
AL 333-95	*Australopithecus afarensis*	3.1 mya	FAPST (26.7); FTST (32.3mm)	McHenry (1988); Ward et al. (2012)
AL 333-107	*Australopithecus afarensis*	3.1 mya	HHAP (39.5mm)	Lovejoy et al. (1982b)

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Table 3.2 – continued from previous page

Fossil Specimen	Designation	Date (mya)	Available Measurements	References
AL 333-131	*Australopithecus afarensis*	3.1 mya	FAPST (29.6mm); FTST (38.9mm)	Ward et al. (2012)
AL 333-140	*Australopithecus afarensis*	3.1 mya	FDAPD (24.2mm); FDTD (25.6mm); FECB (57mm)	Ward et al. (2012)
AL 333-142	*Australopithecus afarensis*	3.1 mya	FAPST (18.9); FTST (26.0mm)	Ward et al. (2012)
AL 333-3	*Australopithecus afarensis*	3.1 mya	FML (386mm); FH (39.5mm); FAPST (27.9mm); FTST (35.0mm)	Geissmann (1986); Lovejoy et al. (1982b); McHenry (1988)
AL 333-4	*Australopithecus afarensis*	3.1 mya	FH (39.4mm); FAPST (25.0mm); FTST (31.4mm)	Lovejoy et al. (1982b)
AL 827-1	*Australopithecus afarensis*	3.1 mya	FH (38.2mm); FAPST (19.2mm); FTST (28.9mm); FDAPD (22.8mm); FTAPD (32.0mm)	Ward et al. (2012)
AL 333w-40	*Australopithecus afarensis*	3.1 mya	FAPST (27.8mm); FTST (35.2)	Lovejoy et al. (1982b); McHenry (1988)
AL 333w-56	*Australopithecus afarensis*	3.1 mya	FDAPD (27.1mm); FDTD (42.9mm)	Lovejoy et al. (1982b)
AL 438-1	*Australopithecus afarensis*	3.1 mya	UML (278mm)	Drapeau et al. (2005)
AL 333x-14	*Australopithecus afarensis*	3.1 mya	RHD (22.2mm)	McHenry (1992a)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
AL 444-14	*Australopithecus afarensis*	3.0 mya	CapH (16.0mm)	Ward et al. (2012)
Sts 34	*Australopithecus africanus*	2.6 mya	FECB (64.0mm)	Walker (1973); Mathers and Henneberg (1995)
MLD 16	*Australopithecus africanus*	2.6 mya	RHD (22.4mm)	McHenry (1974); Herries et al. (2010)
Sts 14	*Australopithecus africanus*	2.6 mya	FML (295mm); FAPST (28.4mm); FTST (22.0mm)	McHenry (1991, 1988)
Stw 25	*Australopithecus africanus*	2.6 mya	FML (320mm)	McHenry (1991)
Stw 99	*Australopithecus africanus*	2.6 mya	FML (380mm)	McHenry (1991)
Sts 392	*Australopithecus africanus*	2.6 mya	FML (311mm)	McHenry (1991)
Stw 443	*Australopithecus africanus*	2.6 mya	FML (359mm)	McHenry (1991)
Kromdraai	*Paranthropus robustus*	2.5 mya	HECB (54mm); HHD (40.0mm)	Day (1986); Patterson and Howells (1967)
KNM-ER 3228	*Homo habilis*	2.0 mya	FML (461mm)	McHenry (1991)
KNM-ER 1475	*Homo sp.*	2.0 mya	FAPST (24.0mm); FTST (28.9mm)	McHenry (1988)
MH1	*Australopithecus sediba*	1.96 mya	HAW (35.3mm); FHD (29.8mm)	Berger et al. (2010)
MH2	*Australopithecus sediba*	1.96 mya	HAW (35.2mm); FHD (32.7mm)	Berger et al. (2010)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
KNM-ER 1472	*Homo habilis*	1.9 mya	FML (401mm); FAPST(21.8mm); FTST (31.4mm)	McHenry (1991, 1988)
KNM-ER 1481	*Homo habilis*	1.9 mya	FML (396mm); FAPST (21.0mm); FTST (31.3mm)	McHenry (1991, 1988)
KNM-ER 1500d	*Paranthropus boisei*	1.9 mya	FML(310mm); FAPST (20.0mm); FTST (25.7mm)	McHenry (1991, 1988)
KNM-ER 1503	*Homo habilis* or *Paranthropus boisei*	1.9 mya	FML (349mm); FAPST (22.3mm); FTST (30.7mm)	McHenry (1991, 1988)
KNM-ER 1504	*Paranthropus boisei*	1.9 mya	HECB (59.9mm); CapH (17.9mm); HAW (39.5mm)	McHenry and Brown (2008)
KNM-ER 6020	*Paranthropus boisei*	1.8 mya	HECB (75.3mm); CapH (23.8mm); HAW (44.7mm)	McHenry and Brown (2008)
KNM-ER 1592	*Homo habilis* or *Paranthropus boisei*	1.9 mya	FML (470mm)	McHenry (1991)
KNM-ER 1809	*Homo habilis* or *Paranthropus boisei*	1.9 mya	FML(310mm); FAPST (20.7mm); FTST (26.5mm)	McHenry (1991, 1988)
KNM-ER 3728	*Homo habilis* or *Paranthropus boisei*	1.9 mya	FML (380mm); FAPST (18.4mm); FTST (30.4mm)	McHenry (1991, 1988)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
KNM-ER 738	*Homo sp.* or *Paranthropus boisei*	1.9 mya	FH (33.5mm); FML (378mm); FAPST (21.7mm); FTST (26.9mm)	McHenry (1988); Geissmann (1986); Walker (1973)
SK 3121	*Paranthropus robustus*	1.9 mya	FH (28.8mm)	Susman et al. (2001); Pickering et al. (2012)
SKW 19	*Paranthropus robustus*	1.9 mya	FH (30.7mm)	Susman et al. (2001); Pickering et al. (2012)
SK 24600	*Paranthropus robustus*	1.9 mya	HECB (44.7mm); CapH (16.5mm); HAW (30.5mm); RHD (17.3mm)	Susman et al. (2001); Pickering et al. (2012); McHenry and Brown (2008)
SKX 2045	*Homo erectus*	1.9 mya	RHD (21.6mm)	Susman et al. (2001); Curnoe (2010)
KNM-ER 815	*Paranthropus sp.*	1.9 mya	FAPST (18.9mm); FTST (26.7mm)	McHenry (1988)
O.H. 53	*Homo habilis* or *Paranthropus boisei*	1.8 mya	FML (360mm)	McHenry (1991)
O.H. 62Y	*Homo habilis*	1.8 mya	FML (315mm); FAPST (21.0mm); FTST (21.0mm)	McHenry (1991, 1988)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Zinjanthropus	*Paranthropus boisei*	1.75 mya	TML (277mm)	Day (1986); Domínguez-Rodrigo et al. (2005)
TM 1517	*Paranthropus robustus*	1.75 mya	HML (263mm); HECB (54.0mm); CapH (16.9mm); HAW (40.1mm)	Susman et al. (2001); Mathers and Henneberg (1995); McHenry and Brown (2008)
KNM-ER 736	*Homo sp.*	1.7 mya	FML (482mm); FAPST (29.9mm); FTST (38.0mm)	McHenry (1988); Geissmann (1986)
KNM-ER 1808	*Homo erectus*	1.7 mya	FML (485mm)	McHenry (1991)
SK 82	*Paranthropus robustus*	1.7 mya	FH (34.4mm); FML (337mm); FAPST (25.0mm); FTST (30.4mm)	Susman et al. (2001); McHenry (1991, 1988)
SK 97	*Paranthropus robustus*	1.7 mya	FH (37.1mm); FML (367mm); FAPST (24.3mm); FTST (32.6mm)	Susman et al. (2001); McHenry (1991, 1988)
SK 18b	*Homo erectus*	1.7 mya	RHD (21.2mm)	McHenry (1974); Mathers and Henneberg (1995)
TM 1513	*Australopithecus africanus*	1.7 mya	FECB (57.0mm)	Walker (1973); Mathers and Henneberg (1995)

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Table 3.2 – continued from previous page

Fossil Specimen	Designation	Date (mya)	Available Measurements	References
O.H. 20	*Paranthropus sp.*	1.7 mya	FAPST (22.8mm); FTST (29.6mm)	McHenry (1988)
Dmanisi 4167	*Homo sp.*	1.7 mya	FH (40.0mm); FML (386mm)	Lordkipanidze et al. (2007); Holloway et al. (2004a)
Dmanisi 4507	*Homo sp.*	1.7 mya	HML (295mm)	Lordkipanidze et al. (2007); Holloway et al. (2004a)
Dmanisi 3901	*Homo sp*	1.7 mya	TML (300mm)	Lordkipanidze et al. (2007); Holloway et al. (2004a)
KNM-ER 3735A	*Homo habilis*	1.6 mya	HECB (57.4mm); CapH (16.4mm); HAW (32.3mm)	McHenry and Brown (2008)
KNM-ER 737	*Homo sp.*	1.6 mya	FML (460mm); FAPST (26.0mm); FTST (38.0mm)	McHenry (1988); Geissmann (1986)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
KNM-WT 15000	*Homo erectus*	1.6 mya	HMSMax (29.9mm); HMSMin (16.7mm); CapH (16.6mm); HECB (55.0mm); (UML (270mm); FML (432mm); FH (46.0mm); FAPST (29.5mm); FTST (31.0mm); TML (380mm)	Walker and Leakey (1993)
KNM-ER 1465	*Paranthropus sp.*	1.6 mya	FAPST (26.2mm); FTST (28.9mm)	McHenry (1988)
KNM-ER 803	*Homo sp.*	1.5 mya	FAPST (26.7mm); FTST (34.5mm)	Geissmann (1986)
KNM-ER 993	*Homo erectus* or *Paranthropus boisei*	1.5 mya	FML (365mm); FAPST (25.2mm); FTST (32.6mm); FECB (69.0mm)	McHenry (1991, 1988); Walker (1973)
KNM-ER 1463	*Homo erectus* or *Paranthropus boisei*	1.5 mya	FML (310mm); FAPST (21.9mm); FTST (27.3mm)	McHenry (1991, 1988)
KNM-ER 1807	Homo erectus or *Paranthropus boisei*	1.5 mya	FML (420mm)	McHenry (1991)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
KNM-ER 739	*Paranthropus boisei*	1.4 mya	HECB (71.2mm); CapH (25.6mm); HAW (43.6mm)	McHenry and Brown (2008); McHenry (1974)
SKX 10924	*Homo erectus*	1.0 mya	HECB (43.8mm); CapH (15.3mm); HAW (31mm)	Susman et al. (2001); McHenry and Brown (2008)
O.H. 34	*Homo erectus*	1 mya	FML (432mm)	McHenry (1991)
Trinil I	*Homo erectus*	1 mya	FML (455mm); FECB (77mm); FHD (44mm)	Kennedy (1983); Day (1986); Henry et al. (2011)
Trinil II	*Homo erectus*	1 mya	FML (500mm)	Feldesman et al. (1990); Henry et al. (2011)
O.H. 28	*Homo erectus*	0.7 mya	FML (456mm)	McHenry (1991)
Peking IV	*Homo erectus*	0.4 mya	FML (407mm)	Feldesman et al. (1990); Steudel-Numbers and Tilkens (2004)
Broken Hill E691	*Homo sapiens*	0.30 mya	FH (52.0mm); TML (416mm)	Trinkaus (2009); Day (1986)
Solo (Ngandong)	*Homo erectus*	0.2 mya	TML (365mm)	Day (1986)
Qafzeh 9	*Homo sapiens*	0.1 mya	FML (469mm)	Feldesman et al. (1990); Steudel-Numbers and Tilkens (2004)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Skhul 4	*Homo sapiens*	0.1 mya	FML (486mm); FAPST (25mm); FTST (31mm); FAPMS (33.2mm); FTMS (26mm)	Feldesman et al. (1990); Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
Skhul 5	*Homo sapiens*	0.1 mya	HML (378mm); FML (515mm); FAPMS (38.6mm); FTMS (27.4mm)	Feldesman et al. (1990); Day (1986); Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
Skhul 7	*Homo sapiens*	0.1 mya	FML (438mm); FAPST (28.2mm); FTST (25.7mm)	Feldesman et al. (1990); Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
Skhul 6	*Homo sapiens*	0.1 mya	FML (475mm); FAPST (25.3mm); FTST (30.1mm); FAPMS (36.9mm); FTMS (27.3mm)	Feldesman et al. (1990); Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
Skhul 3	*Homo sapiens*	0.1 mya	FAPMS (36mm); FTMS (30.6mm)	Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
Skhul 9	*Homo sapiens*	0.1 mya	FAPST(29.3mm); FTST (38.3mm)	Trinkaus (1976); Steudel-Numbers and Tilkens (2004)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Krapina I	*Homo neanderthalensis*	0.1 mya	FH (52.7mm)	Day (1986); Smith et al. (2010)
Krapina II	*Homo neanderthalensis*	0.1 mya	FH (44.3mm)	Day (1986); Smith et al. (2010)
Krapina 213	*Homo neanderthalensis*	0.1 mya	FAPST (27.1mm); FTST (36mm)	Trinkaus (1976); Smith et al. (2010)
Krapina 214	*Homo neanderthalensis*	0.1 mya	FAPST (21.4mm); FTST (29.1mm)	Trinkaus (1976); Smith et al. (2010)
Tabun C1	*Homo neanderthalensis*	0.075 mya	HML (287mm); RML (222mm); UML (243mm); FML (410mm); FAPST (22.6mm); FTST (30.4mm); FAPMS (24mm); FTMS (27.4mm); TML (310mm)	Feldesman et al. (1990); Day (1986); Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
Tabun C3	*Homo neanderthalensis*	0.075 mya	FAPMS (22.2mm); FTMS (24.1mm)	Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
Tabun E1	*Homo neanderthalensis*	0.075 mya	FAPST (25mm); FTST (26mm); FTMS (28mm)	Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
Kebarah M1	*Homo sapiens*	0.06 mya	FAPMS (27.3mm); FTMS (24mm)	Trinkaus (1976); Schwarcz et al. (1989)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Kebarah M4	*Homo sapiens*	0.06 mya	FAPMS (28.4mm); FTMS (21.3mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah M7	*Homo sapiens*	0.06 mya	FAPMS (27.1mm); FTMS (23.5mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P2	*Homo sapiens*	0.06 mya	FAPST (22.6mm); FTST (28.7mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P3	*Homo sapiens*	0.06 mya	FAPST (19.9mm); FTST (27mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P5	*Homo sapiens*	0.06 mya	FAPST (24.5mm); FTST (33.9mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P6	*Homo sapiens*	0.06 mya	FAPST (19.1mm); FTST (27.2mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P7	*Homo sapiens*	0.06 mya	FAPST (20.4mm); FTST (26mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P8	*Homo sapiens*	0.06 mya	FAPST (19.6mm); FTST (26.5mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P9	*Homo sapiens*	0.06 mya	FAPST (22.8mm); FTST (27.4mm)	Trinkaus (1976); Schwarcz et al. (1989)

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Table 3.2 – continued from previous page

Fossil Specimen	Designation	Date (mya)	Available Measurements	References
Kebarah P10	*Homo sapiens*	0.06 mya	FAPST (19.6mm); FTST (26mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P11	*Homo sapiens*	0.06 mya	FAPST (21.7mm); FTST (29.1mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P12	*Homo sapiens*	0.06 mya	FAPST (21.8mm); FTST (32.4)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P13	*Homo sapiens*	0.06 mya	FAPST (18.1mm); FTST (28.4mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P14	*Homo sapiens*	0.06 mya	FAPST (24.8mm); FTST (32mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P16	*Homo sapiens*	0.06 mya	FAPST (20.6mm); FTST (26.7mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P17	*Homo sapiens*	0.06 mya	FAPST (19.1mm); FTST (28.2mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P20	*Homo sapiens*	0.06 mya	FAPST (23.8mm); FTST (31.3mm)	Trinkaus (1976); Schwarcz et al. (1989)
Kebarah P22	*Homo sapiens*	0.06 mya	FAPST (21.7mm); FTST (30.3mm)	Trinkaus (1976); Schwarcz et al. (1989)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Kebarah P24	*Homo sapiens*	0.06 mya	FAPMS (30mm); FTMS (29.2)	Trinkaus (1976); Schwarcz et al. (1989)
Neanderthal	*Homo neanderthalensis*	0.055 mya	HML (312mm); RML (239mm); FML (438mm); FAPST (29mm); FTST (32.8mm); FAPMS (31.3mm); FTMS (28.2mm)	Day (1986); Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
Amud I	*Homo neanderthalensis*	0.054 mya	FML (482mm); FAPST (29.4mm); FTST (36.9mm); FAPMS (32.3mm); FTMS (32.4mm)	Feldesman et al. (1990); Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
La Chapelle	*Homo neanderthalensis*	0.05 mya	HML (313mm); RML (235mm); FML (430mm); FAPST (31.0mm); FTST (29.0mm); FAPMS (31.1mm); FTMS (29.1mm)	Feldesman et al. (1990); Day (1986); Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
Palomas 96	*Homo neanderthalensis*	0.05 mya	HML (272.0mm); RML (206.0mm)	Walker et al. (2011)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
La Quina 5	*Homo neanderthalensis*	0.05 mya	FAPST (26mm); FTST (33.5mm); FAPMS (26mm); FTMS (30mm)	Trinkaus (1976); Smith et al. (2010)
La Quina unn (B2)	*Homo neanderthalensis*	0.05 mya	FAPST (26.8mm); FTST (34.5mm)	Trinkaus (1976); Smith et al. (2010)
St. Germain la Rive	*Homo sapiens*	0.04 mya	FML (408mm); FAPST (23mm); FTST (31mm); FAPMS (29.5mm); FTMS (25mm)	Feldesman et al. (1990); Trinkaus (1976); Mathers and Henneberg (1995)
Tagliente I	*Homo sapiens*	0.04 mya	FML (431mm)	Feldesman et al. (1990); Mathers and Henneberg (1995)
Veryier	*Homo sapiens*	0.04 mya	FML (459mm); FAPST (26mm); FTST (34mm); FAPMS (28.5mm); FTMS (23.5mm)	Feldesman et al. (1990); Trinkaus (1976); Mathers and Henneberg (1995)
Shanidar 1	*Homo neanderthalensis*	0.044 mya	FML (458mm)	Feldesman et al. (1990); Henry et al. (2011)
Shanidar 4	*Homo neanderthalensis*	0.044 mya	FML (422mm); FAPST (25mm); FTST (31mm)	Feldesman et al. (1990); Trinkaus (1976); Henry et al. (2011)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Shanidar 5	*Homo neanderthalensis*	0.044 mya	FML (447mm)	Feldesman et al. (1990); Henry et al. (2011)
Shanidar 6	*Homo neanderthalensis*	0.044 mya	FML (384mm)	Feldesman et al. (1990); Henry et al. (2011)
La Ferrassie 1	*Homo neanderthalensis*	0.038 mya	FML (458mm); FAPST (29.9mm); FTST (38mm)	Feldesman et al. (1990); Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
La Ferrassie 2	*Homo neanderthalensis*	0.038 mya	FML (407mm); FAPST (27.9mm); FTST (32mm)	Feldesman et al. (1990); Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
Spy 2	*Homo neanderthalensis*	0.036 mya	FML (423mm); FAPST (28.4mm); FTST (35mm); FAPMS (29.3mm); FMST (29.1mm)	Feldesman et al. (1990); Trinkaus (1976); Henry et al. (2011)
Font de foret I	*Homo neanderthalensis*	0.02 mya	FML (424mm); FAPMS (33mm); FTMS (30.3mm)	Feldesman et al. (1990); Trinkaus (1976); Mathers and Henneberg (1995)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Cro Magnon 1	*Homo sapiens*	0.03 mya	FAPST (30.5mm); FTST (38.5mm); FAPMS (40mm); FTMS (31mm)	Trinkaus (1976); Steudel-Numbers and Tilkens (2004)
Cro Magnon 3	*Homo sapiens*	0.03 mya	FML (485mm)	Feldesman et al. (1990); Steudel-Numbers and Tilkens (2004)
Baousso de Torre 1	*Homo sapiens*	0.03 mya	FML (535mm)	Feldesman et al. (1990); Villotte and Henry-Gambier (2010)
Baousso de Torre 2	*Homo sapiens*	0.03 mya	FML (504mm)	Feldesman et al. (1990); Villotte and Henry-Gambier (2010)
Barma Grande 1	*Homo sapiens*	0.03 mya	FML (532mm); FAPST (29.5mm); FTST (42.5mm)	Feldesman et al. (1990); Trinkaus (1976); Trinkaus et al. (2006)
Barma Grande 2	*Homo sapiens*	0.03 mya	FML (491mm); FAPST (22mm); FTST (40.5mm)	Feldesman et al. (1990); Trinkaus (1976); Trinkaus et al. (2006)
Barma Grande 5	*Homo sapiens*	0.03 mya	FML (495mm)	Feldesman et al. (1990); Trinkaus et al. (2006)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Grotte des Enfants 1	*Homo sapiens*	0.03 mya	FAPST (29.5mm); FTST (38.5mm)	Trinkaus (1976); Trinkaus et al. (2006)
Grotte des Enfants 3	*Homo sapiens*	0.03 mya	FAPST (21mm); FTST (29mm)	Trinkaus (1976); Trinkaus et al. (2006)
Grotte des Enfants 4	*Homo sapiens*	0.03 mya	FML (523mm); FAPST (33mm); FTST (39mm)	Feldesman et al. (1990); Trinkaus (1976); Trinkaus et al. (2006)
Grotte des Enfants 5	*Homo sapiens*	0.03 mya	FML (434mm)	Feldesman et al. (1990); Trinkaus et al. (2006)
Predmost 3	*Homo sapiens*	0.03 mya	FML (484mm); FAPST (24mm); FTST (38mm); FAPMS (30.8mm); FTMS (30mm)	Feldesman et al. (1990); Trinkaus (1976); Trinkaus et al. (2006)
Predmost 4	*Homo sapiens*	0.03 mya	FML (418mm); FAPST (25mm); FTST (35.8mm); FAPMS (29mm); FTMS (28mm)	Feldesman et al. (1990); Trinkaus (1976); Trinkaus et al. (2006)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Predmost 9	*Homo sapiens*	0.03 mya	FML (447mm); FAPST (23mm); FTST (33mm); FAPMS (27mm); FTMS (25mm)	Feldesman et al. (1990); Trinkaus (1976); Trinkaus et al. (2006)
Predmost 10	*Homo sapiens*	0.03 mya	FML (407mm); FAPST (22.6mm); FTST (35mm); FAPMS (25.4mm); FTMS (27.5mm)	Feldesman et al. (1990); Trinkaus (1976); Trinkaus et al. (2006)
Predmost 14	*Homo sapiens*	0.03 mya	FML (449mm); FAPST (22.5mm); FTST (33mm); FAPMS (26.4mm); FTMS (26.4mm)	Feldesman et al. (1990); Trinkaus (1976); Trinkaus et al. (2006)
Paglicci I	*Homo sapiens*	0.03 mya	FML (452mm); FAPST (28.3mm); FTST (38mm); FAPMS (38.3mm); FTMS (30.4mm)	Feldesman et al. (1990); Trinkaus (1976); Trinkaus et al. (2006)
Paviland I	*Homo sapiens*	0.03 mya	FML (476mm); FAPST (27mm); FTST (36mm); FAPMS (32.5mm); FTMS (27.5mm)	Feldesman et al. (1990); Trinkaus (1976); Trinkaus et al. (2006)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Mladeč 1	*Homo sapiens*	0.03 mya	FAPST (24mm); FTST (34mm)	Trinkaus (1976); Trinkaus et al. (2006)
Mladeč 6	*Homo sapiens*	0.03 mya	FAPMS (37mm); FTMS (26mm)	Trinkaus (1976); Trinkaus et al. (2006)
La Rochette 1	*Homo sapiens*	0.03 mya	FAPST (26.5mm); FTST (33mm); FAPMS (29mm); FTMS (26mm)	Trinkaus (1976); Trinkaus et al. (2006)
Willendorf 1	*Homo sapiens*	0.03 mya	FAPMS(28mm); FTMS (24mm)	Trinkaus (1976); Trinkaus et al. (2006)
Caviglione I	*Homo sapiens*	0.02 mya	FML (470mm)	Feldesman et al. (1990); Mathers and Henneberg (1995)
Bruniquel 24	*Homo sapiens*	0.02 mya	FML (409mm)	Feldesman et al. (1990); Mathers and Henneberg (1995)
Cap Blanc I	*Homo sapiens*	0.021 mya	FML (419mm); FAPST (21.6mm); FTST (28.4mm); FAPMS (28mm); FTMS (23mm)	Feldesman et al. (1990); Trinkaus (1976); Mathers and Henneberg (1995)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Pataud 10	*Homo sapiens*	0.021 mya	FAPMS (30mm); FTMS (27mm)	Trinkaus (1976)
La Madelaine	*Homo sapiens*	0.02 mya	FML (460mm); FAPMS (31mm); FTMS (26mm)	Feldesman et al. (1990); **?**); Trinkaus (1976); Mathers and Henneberg (1995)
Brno 2	*Homo neanderthalensis*	0.018 mya	FAPST (28mm); FTST (36.5mm); FAPMS (37mm); FTMS (29mm)	Trinkaus (1976, 2005)
LB1	*Homo floresiensis*	0.018 mya	HMSMax (17.44mm); HMSMin (16.35mm); FML (280mm); FHD (31.0mm); FAPST (19.96mm); FTST (24.54mm); FAPMS (21.83mm); FTMS (21.39)	Jungers et al. (2009)
Chancellade	*Homo sapiens*	0.017 mya	FML (408mm); FAPST (25mm); FTST (35mm); FAPMS (30mm); FTMS (28mm)	Feldesman et al. (1990); Trinkaus (1976)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Le Peyrat 5	*Homo sapiens*	0.017 mya	FML (433mm); FAPST (31.5mm); FTST (31.8mm); FAPMS (35.8mm); FTMS (28mm)	Trinkaus (1976); Formicola and Giannecchini (1999)
Le Peyrat 6	*Homo sapiens*	0.017 mya	FML (422mm); FAPST (24.8mm); FTST (27.4mm); FAPMS (24mm); FTMS (23.5mm)	Trinkaus (1976); Formicola and Giannecchini (1999)
Ehringsdorf 5	*Homo neanderthalensis*	0.015 mya	FAPST (26.8mm); FTST (37.1mm); FAPMS (31.5mm); FTMS (31.1mm)	Trinkaus (1976); Bischoff et al. (2007)
Obercassel I	*Homo sapiens*	0.015 mya	FML (444mm); FAPST (25mm); FTST (32mm); FAPMS (25mm); FTMS (25mm)	Feldesman et al. (1990); Trinkaus (1976); Mathers and Henneberg (1995)
Obercassel 2	*Homo sapiens*	0.015 mya	FML (430mm); FAPST (30mm); FTST (43mm)	Feldesman et al. (1990); Trinkaus (1976); Mathers and Henneberg (1995)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
San Teodoro 4	*Homo sapiens*	0.011 mya	FML (425mm); FAPST (27mm); FTST (37mm); FAPMS (30mm); FTMS (29mm)	Trinkaus (1976); Holt (2003)
San Teodoro 1	*Homo sapiens*	0.01 mya	FML (442mm); FAPST (31.5mm); FTST (38mm); FAPMS (35mm); FTMS (30mm)	Trinkaus (1976)
Belt Cave 1	*Homo sapiens*	0.009 mya	FAPST (20.7mm); FTST (25.5mm)	Trinkaus (1976); Coon (1952)
Belt Cave 3	*Homo sapiens*	0.009 mya	FAPST (23.7mm); FTST (33.1mm)	Trinkaus (1976); Coon (1952)
Hotu 2	*Homo sapiens*	0.009 mya	FML (455mm); FAPST (25.5mm); FTST (31mm); FAPMS (31mm); FTMS (26.5mm)	Trinkaus (1976); Coon (1952)
Hotu 3	*Homo sapiens*	0.009 mya	FAPST (22.5mm); FTST (28.5mm); FAPMS (26mm); FTMS (24mm)	Trinkaus (1976); Coon (1952)
Combe-Capelle 1	*Homo sapiens*	0.007 mya	FML (423mm); FAPST (25mm); FTST (29mm)	Feldesman et al. (1990); Trinkaus (1976); Hoffmann et al. (2011)

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Table 3.2 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Available Measurements**	**References**
Culoz 1	*Homo sapiens*	0.007 mya	FML (426mm); FAPST (27mm); FTST (33mm); FAPMS (33mm); FTMS (26mm)	Trinkaus (1976); Holt (2003)
Culoz 2	*Homo sapiens*	0.007 mya	FML (440mm); FAPST (23mm); FTST (32mm); FAPMS (29mm); FTMS (25mm)	Trinkaus (1976); Holt (2003)
Gramat 1	*Homo sapiens*	0.007 mya	FML (447mm)	Trinkaus (1976); Holt (2003)
Montardit 3	*Homo sapiens*	0.007 mya	FML (407mm); FAPST (22mm); FTST (28mm); FAPMS (27mm); FTMS (23mm)	Trinkaus (1976); Holt (2003)
Biscegli I	*Homo neanderthalensis*	0.064 mya	FAPMS (29.5mm); FTMS (28.8mm)	Trinkaus (1976)
Sedia-del-Diavolo	*Homo neanderthalensis*	0.07 mya	FAPMS (31mm); FTMS (29mm)	Trinkaus (1976)
Hortus 34	*Homo neanderthalensis*	0.04 mya	FAPST (24mm); FTST (30mm)	Trinkaus (1976)
Sandalja I	*Homo sapiens*	0.0123 mya	FAPST (23.7mm); FTST (30.4mm)	Trinkaus (1976)

The postcranial measurements were used to estimate body mass for each specimen. Final body mass estimates used in analyses are found in Table 3.3. Bolded values in the table were eliminated from analyses

because they are unrealistic body mass estimates, generally because of allometric differences between the fossil specimen and the human reference sample. See the"Body Mass Estimation" methods section and the "Results" chapter for more information on the estimation of these body masses.

Two subsets were used in some analyses. One subset contains only *Homo* specimens from ca. 2 mya to present (Table 3.4). Additionally, analyses included a subset of "purported ancestors" (Table 3.5). "Purported ancestors" include *Australopithecus africanus* and all *Homo* specimens. *Australopithecus afarensis* and *Paranthropus* specimens are excluded. Many *Paranthropus* specimens are contemporary with *Homo* so they cannot be ancestral. Analysis, particularly of the brain, suggest that *Australopithecus africanus* is ancestral to *Homo* (Falk et al., 2000).

3.2 Methods

3.2.1 Body Mass Estimation

Profile likelihood, classical calibration, and inverse calibration estimates were calculated for each fossil hominin specimen. For specimens with multiple postcranial measurements available R and Rx statistics, R and Rx p-values, and z-scores were calculated.

Several criteria guide the decision of which body mass estimate to use in subsequent analyses. If an individual specimen has non-significant R and Rx p-values, it is assumed that the individual comes from the same allometric and size distribution as the reference sample. Thus, the reference sample forms a reasonable prior and inverse calibration, because it is Bayesian, should give the best estimate.

Sundberg and Brown (1989, p. 352) suggest that "In practice if R is large one would probably wish to see whether particular individual components of $\hat{\Gamma}^{-\frac{1}{2}}(Z - \hat{\alpha} - \hat{B}\hat{\xi})$ are large." I refer to these vector components as "allometric values." A positive value indicates a particular measure for a fossil specimen is "too large" if the fossil was scaling allometrically with the reference sample. Likewise, negative values indicate a measure that is "too small." The sum of the squared elements is equal to the R statistic, so the threshold value for "too large" or "too small" is 1.96 (the 95% critical value from a chi-square with one degree of freedom). R is only calculated for individuals with two or more available measurements because it requires a variance-covariance matrix.

Looking at Darroch and Mosimann (1985) log shape variables is another way of assessing the contribution of individual measurements on a specimen's overall allometric departure from the reference sample. The log size of an individual is defined by the average of its log bone measurements (number varies per specimen). The log shape variables are the individual log measurements minus the individual's log size, which is an

"internal measure" of size (Jungers et al., 1995). These variables are given as z-scores for each measurement. As with the allometry values, positive z-scores indicate a measurement is relatively "too big," while negative z-scores indicate a measurement is relatively "too small"(Uhl et al., 2013). Because the z-scores require an "internal measure" of size they require at least three variables. For specimens with only two measurements only allometric values are given because the z-scores are uninformative in that case (they have equal absolute values on either side of zero).

Measurements with large positive or negative allometry or z-score values can be individually removed to improve the allometric fit of an individual relative to the reference sample. This would manifest as a lower R score, thus narrowing the confidence interval and increasing confidence in the estimate. All scores and estimates are given in Chapter 4, but Table 3.3, Table 3.4, and Table 3.5 give the final body mass estimates used in subsequent analyses.

Table 3.3: Final Body Mass Estimates

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
KNM-KP 271	*Australopithecus anamensis*	4.1	55.3	Inverse calibration
Stw 431	*Australopithecus africanus*	4.0	51.4	Inverse calibration
KSD-VP-1/1	*Australopithecus afarensis*	3.58	46.7	Inverse calibration
AL 137-50	*Australopithecus afarensis*	3.4	45.5	Inverse calibration
MAK-VP-1/3	*Australopithecus afarensis*	3.4	46.8	Inverse calibration
AL 152-2	*Australopithecus afarensis*	3.1	**2.0**	Profile likelihood
AL 211-1	*Australopithecus afarensis*	3.1	**3.8**	Profile likelihood

Continued on next page

Table 3.3 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
AL 223-23	*Australopithecus afarensis*	3.1	**3.5**	Profile likelihood
AL 288-1	*Australopithecus afarensis*	3.1	**0.8**	Profile likelihood
AL 322-1	*Australopithecus afarensis*	3.1	**4.5**	Profile likelihood
AL 333-107	*Australopithecus afarensis*	3.1	30.0	Inverse calibration
AL 333-142	*Australopithecus afarensis*	3.1	**1.9**	Profile likelihood
AL 333-3	*Australopithecus afarensis*	3.1	48.6	Inverse calibration
AL 333-4	*Australopithecus afarensis*	3.1	45.6	Inverse calibration
AL 333-95	*Australopithecus afarensis*	3.1	53.7	Inverse calibration
AL 333x-14	*Australopithecus afarensis*	3.1	42.7	Inverse calibration
AL 438-1	*Australopithecus afarensis*	3.1	70.7	Inverse calibration
AL 444-14	*Australopithecus afarensis*	3.0	**0.03**	Profile likelihood
Sts 34	*Australopithecus africanus*	2.6	**12850.7**	Profile likelihood
Sts 392	*Australopithecus africanus*	2.6	28.0	Classical calibration

Continued on next page

Table 3.3 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Stw 25	*Australopithecus africanus*	2.6	29.5	Inverse calibration
Stw 443	*Australopithecus africanus*	2.6	36.5	Classical calibration
Stw 99	*Australopithecus africanus*	2.6	40.5	Inverse calibration
Kromdraai	*Paranthropus robustus*	2.5	51.3	Inverse calibration
KNM-ER 1475	*Homo sp.*	2.0	48.8	Inverse calibration
KNM-ER 3228	*Homo habilis*	2.0	58.0	Classical calibration
MH1	*Australopithecus sediba*	1.96	**2.21**	Classical calibration
MH2	*Australopithecus sediba*	1.96	**4.21**	Classical calibration
KNM-ER 1472	*Homo habilis*	1.9	**7.9**	Profile likelihood
KNM-ER 1481	*Homo habilis*	1.9	**6.1**	Profile likelihood
KNM-ER 1504	*Paranthropus boisei*	1.9	48.5	Inverse calibration
KNM-ER 1592	*Homo habilis* or *Paranthropus boisei*	1.9	60.1	Inverse calibration
KNM-ER 1809	*Homo habilis* or *Paranthropus boisei*	1.9	**4.2**	Profile likelihood
KNM-ER 3728	*Homo habilis* or *Paranthropus boisei*	1.9	**2.4**	Profile likelihood

Continued on next page

Table 3.3 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
KNM-ER 738	*Homo habilis* or *Paranthropus boisei*	1.9	**4.0**	Profile likelihood
KNM-ER 815	*Paranthropus sp.*	1.9	**1.8**	Profile likelihood
SK 24600	*Paranthropus robustus*	1.9	**3.3**	Profile likelihood
SK 3121	*Paranthropus robustus*	1.9	**0.3**	Profile likelihood
SKW 19	*Paranthropus robustus*	1.9	**0.7**	Profile likelihood
SKX 2045	*Homo erectus*	1.9	22.7	Inverse calibration
OH 53	*Homo habilis* or *Paranthropus boisei*	1.8	36.7	Inverse calibration
OH 62Y	*Homo habilis*	1.8	**3.9**	Profile likelihood
TM 1517	*Paranthropus robustus*	1.75	**7.2**	Profile likelihood
Zinjanthropus	*Paranthropus boisei*	1.75	22.9	Inverse calibration
Dmanisi 3901	*Homo sp.*	1.7	28.8	Inverse calibration
Dmanisi 4167	*Homo sp.*	1.7	46.6	Inverse calibration
Dmanisi 4507	*Homo sp.*	1.7	46.4	Classical calibration
KNM-ER 1808	*Homo erectus*	1.7	63.7	Classical calibration
KNM-ER 736	*Homo sp.*	1.7	60.6	Inverse calibration
SK 18b	*Homo erectus*	1.7	**14.8**	Profile likelihood

Continued on next page

Table 3.3 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
SK 97	*Paranthropus robustus*	1.7	**9.3**	Profile likelihood
TM 1513	*Australopithecus africanus*	1.7	**2793.0**	Profile likelihood
KNM-ER 3735A	*Homo habilis*	1.6	**4.5**	Profile likelihood
KNM-ER 737	*Homo sp.*	1.6	54.2	Inverse calibration
KNM-ER 15000	*Homo erectus*	1.6	54.2	Inverse calibration
OH 20	*Paranthropus sp.*	1.6	46.7	Inverse calibration
KNM-ER 1465	*Paranthropus sp.*	1.6	52.6	Inverse calibration
KNM-ER 993	*Homo erectus* or *Paranthropus boisei*	1.5	51.1	Inverse calibration
KNM-ER 6020	*Paranthropus boisei*	1.4	60.0	Inverse calibration
KNM-ER 739	*Paranthropus boisei*	1.4	**306.8**	Profile likelihood
OH 34	*Homo erectus*	1.0	51.4	Inverse calibration
SKX 10924	*Homo erectus*	1.0	**2.7**	Profile likelihood
Trinil I	*Homo erectus*	1.0	54.9	Inverse calibration
Trinil II	*Homo erectus*	1.0	67.4	Classical calibration
OH 28	*Homo erectus*	0.7	56.8	Inverse calibration
Peking IV	*Homo erectus*	0.04	46.0	Classical calibration
Broken Hill E691	*Homo sapiens*	0.3	68.6	Inverse calibration
Solo (Ngandong)	*Homo erectus*	0.2	50.6	Classical calibration

Continued on next page

Table 3.3 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Krapina 214	*Homo neanderthalensis*	0.1	**5.4**	Profile likelihood
Krapina I	*Homo neanderthalensis*	0.1	**404.7**	Profile likelihood
Krapina II	*Homo neanderthalensis*	0.1	51.3	Classical calibration
Qafzeh IX	*Homo sapiens*	0.1	59.8	Classical calibration
Skhul III	*Homo sapiens*	0.1	64.7	Inverse calibration
Skhul IV	*Homo sapiens*	0.1	52.5	Inverse calibration
Skhul VI	*Homo sapiens*	0.1	54.4	Inverse calibration
Skhul VII	*Homo sapiens*	0.1	48.8	Inverse calibration
Tabun C1	*Homo neanderthalensis*	0.075	48.3	Inverse calibration
Tabun C3	*Homo neanderthalensis*	0.075	**16.3**	Profile likelihood
Tabun E1	*Homo neanderthalensis*	0.075	51.4	Inverse calibration
Sedia-del-Diavolo	*Homo neanderthalensis*	0.07	57.8	Inverse calibration
Biscegli I	*Homo neanderthalensis*	0.064	56.4	Inverse calibration
Kebarah M1	*Homo sapiens*	0.06	45.1	Inverse calibration
Kebarah M4	*Homo sapiens*	0.06	**13.9**	Profile likelihood
Kebarah M7	*Homo sapiens*	0.06	44.0	Inverse calibration
Kebarah P10	*Homo sapiens*	0.06	**2.6**	Profile likelihood
Kebarah P11	*Homo sapiens*	0.06	**6.1**	Profile likelihood
Kebarah P14	*Homo sapiens*	0.06	50.4	Inverse calibration

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Table 3.3 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Kebarah P16	*Homo sapiens*	0.06	**4.0**	Profile likelihood
Kebarah P2	*Homo sapiens*	0.06	**9.0**	Profile likelihood
Kebarah P20	*Homo sapiens*	0.06	48.6	Inverse calibration
Kebarah P24	*Homo sapiens*	0.06	59.1	Inverse calibration
Kebarah P3	*Homo sapiens*	0.06	**2.9**	Profile likelihood
Kebarah P6	*Homo sapiens*	0.06	**1.9**	Profile likelihood
Kebarah P7	*Homo sapiens*	0.06	**3.7**	Profile likelihood
Kebarah P8	*Homo sapiens*	0.06	**2.6**	Profile likelihood
Kebarah P9	*Homo sapiens*	0.06	46.6	Inverse calibration
Neanderthal I	*Homo neanderthalensis*	0.055	55.4	Inverse calibration
Amud I	*Homo neanderthalensis*	0.054	67.1	Inverse calibration
La Chapelle	*Homo sapiens*	0.05	56.2	Inverse calibration
La Quina 5	*Homo neanderthalensis*	0.05	55.7	Inverse calibration
Palomas 96	*Homo neanderthalensis*	0.05	**9.6**	Profile likelihood
Shanidar I	*Homo neanderthalensis*	0.044	57.3	Classical calibration
Shanidar IV	*Homo neanderthalensis*	0.044	48.9	Inverse calibration
Shanidar V	*Homo neanderthalensis*	0.044	54.7	Classical calibration
Shanidar VI	*Homo neanderthalensis*	0.044	41.3	Classical calibration

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Table 3.3 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Hortus 34	*Homo neanderthalensis*	0.04	48.8	Inverse calibration
St. Germaine la Rive	*Homo sapiens*	0.04	45.1	Inverse calibration
Tagliente I	*Homo sapiens*	0.04	51.2	Classical calibration
Veryier	*Homo sapiens*	0.04	45.1	Inverse calibration
La Ferrassie 1	*Homo neanderthalensis*	0.038	58.7	Inverse calibration
La Ferrassie 2	*Homo neanderthalensis*	0.038	50.8	Inverse calibration
Spy 2	*Homo neanderthalensis*	0.036	55.5	Inverse calibration
Baousso de Torre I	*Homo sapiens*	0.03	76.3	Classical calibration
Baousso de Torre II	*Homo sapiens*	0.03	68.4	Classical calibration
Barma Grande V	*Homo sapiens*	0.03	66.1	Classical calibration
Cro Magnon 1	*Homo sapiens*	0.03	64.7	Inverse calibration
Cro Magnon 3	*Homo sapiens*	0.03	63.7	Classical calibration
Grotte des Enfants III	*Homo sapiens*	0.03	**4.5**	Profile likelihood
Grotte des Enfants IV	*Homo sapiens*	0.03	**324.2**	Profile likelihood
Grotte des Enfants V	*Homo sapiens*	0.03	51.8	Classical calibration
La Rochette 1	*Homo sapiens*	0.03	50.4	Inverse calibration
Paglicci I	*Homo sapiens*	0.03	59.1	Inverse calibration
Paviland I	*Homo sapiens*	0.03	56.0	Inverse calibration
Predmost III	*Homo sapiens*	0.03	63.2	Inverse calibration
Predmost IV	*Homo sapiens*	0.03	51.2	Inverse calibration
Predmost IX	*Homo sapiens*	0.03	46.5	Inverse calibration
Predmost X	*Homo sapiens*	0.03	48.0	Inverse calibration
Predmost XIV	*Homo sapiens*	0.03	51.3	Inverse calibration

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Table 3.3 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
San Teodoro 4	*Homo sapiens*	0.03	54.4	Inverse calibration
Willendorf 1	*Homo sapiens*	0.03	45.5	Inverse calibration
Brno 2	*Homo neanderthalensis*	0.024	58.4	Inverse calibration
Cap Blanc I	*Homo sapiens*	0.021	41.3	Inverse calibration
Pataud 10	*Homo sapiens*	0.021	52.9	Inverse calibration
Bruniquel XXIV	*Homo sapiens*	0.02	46.4	Classical calibration
Caviglione I	*Homo sapiens*	0.02	60.1	Classical calibration
Font de foret I	*Homo neanderthalensis*	0.02	62.0	Inverse calibration
La Madelaine	*Homo sapiens*	0.02	51.7	Inverse calibration
LB1	*Homo floresiensis*	0.018	**9.3**	Profile likelihood
Chancellade	*Homo sapiens*	0.017	50.7	Inverse calibration
Le Peyrat 5	*Homo sapiens*	0.017	54.6	Inverse calibration
Le Peyrat 6	*Homo sapiens*	0.017	42.6	Inverse calibration
Ehringsdorf 5	*Homo neanderthalensis*	0.015	60.8	Inverse calibration
Obercassel I	*Homo sapiens*	0.015	47.3	Inverse calibration
Obercassel II	*Homo sapiens*	0.015	55.8	Inverse calibration
Sandalja I	*Homo sapiens*	0.0123	48.3	Inverse calibration
San Teodoro 1	*Homo sapiens*	0.01	60.6	Inverse calibration
Belt Cave 1	*Homo sapiens*	0.009	**4.2**	Profile likelihood
Hotu 2	*Homo sapiens*	0.009	51.1	Inverse calibration
Hotu 3	*Homo sapiens*	0.009	43.2	Inverse calibration
Combe-Capelle 1	*Homo sapiens*	0.007	49.2	Inverse calibration
Culoz 1	*Homo sapiens*	0.007	49.7	Inverse calibration

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Table 3.3 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Culoz 2	*Homo sapiens*	0.007	47.0	Inverse calibration
Gramat 1	*Homo sapiens*	0.007	54.7	Classical calibration
Montardit 3	*Homo sapiens*	0.007	**15.5**	Profile likelihood

Table 3.4: Final Body Mass Estimates, 2mya—present

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
KNM-ER 1475	*Homo sp.*	2.0	48.8	Inverse calibration
KNM-ER 3228	*Homo habilis*	2.0	58.0	Classical calibration
KNM-ER 1592	*Homo habilis* or *Paranthropus boisei*	1.9	60.1	Classical calibration
OH 53	*Homo habilis* or *Paranthropus boisei*	1.8	36.7	Inverse calibration
Dmanisi 4167	*Homo sp.*	1.7	46.6	Inverse calibration
Dmanisi 4507	*Homo sp.*	1.7	46.4	Classical calibration
KNM-ER 1808	*Homo erectus*	1.7	63.7	Classical calibration
KNM-ER 736	*Homo sp.*	1.7	60.6	Inverse calibration
KNM-ER 737	*Homo sp.*	1.6	54.2	Inverse calibration
KNM-ER 15000	*Homo erectus*	1.6	54.2	Inverse calibration
OH 34	*Homo erectus*	1.0	51.4	Classical calibration
Trinil I	*Homo erectus*	1.0	54.9	Inverse calibration
Trinil II	*Homo erectus*	1.0	67.4	Classical calibration
OH 28	*Homo erectus*	0.7	56.8	Classical calibration

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Table 3.4 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Peking IV	*Homo erectus*	0.04	46.0	Classical calibration
Broken Hill E691	*Homo sapiens*	0.3	68.6	Inverse calibration
Solo (Ngandong)	*Homo erectus*	0.2	50.6	Inverse calibration
Ehringsdorf 5	*Homo neanderthalensis*	0.15	60.8	Inverse calibration
Krapina II	*Homo neanderthalensis*	0.1	51.3	Classical calibration
Qafzeh IX	*Homo sapiens*	0.1	59.8	Classical calibration
Skhul III	*Homo sapiens*	0.1	64.7	Inverse calibration
Skhul IV	*Homo sapiens*	0.1	52.5	Inverse calibration
Skhul VI	*Homo sapiens*	0.1	54.4	Inverse calibration
Skhul VII	*Homo sapiens*	0.1	48.8	Inverse calibration
Tabun C1	*Homo neanderthalensis*	0.075	48.3	Inverse calibration
Tabun E1	*Homo neanderthalensis*	0.075	51.4	Inverse calibration
Sedia-del-Diavolo	*Homo neanderthalensis*	0.07	57.8	Inverse calibration
Biscegli I	*Homo neanderthalensis*	0.064	56.4	Inverse calibration
Kebarah M1	*Homo sapiens*	0.06	45.1	Inverse calibration
Kebarah M7	*Homo sapiens*	0.06	44.0	Inverse calibration
Kebarah P14	*Homo sapiens*	0.06	50.4	Inverse calibration
Kebarah P20	*Homo sapiens*	0.06	48.6	Inverse calibration
Kebarah P24	*Homo sapiens*	0.06	59.1	Inverse calibration
Kebarah P9	*Homo sapiens*	0.06	46.6	Inverse calibration

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Table 3.4 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Neanderthal I	*Homo neanderthalensis*	0.055	55.4	Inverse calibration
Amud I	*Homo neanderthalensis*	0.054	67.1	Inverse calibration
La Chapelle	*Homo sapiens*	0.05	56.2	Inverse calibration
La Quina 5	*Homo neanderthalensis*	0.05	55.7	Inverse calibration
Shanidar I	*Homo neanderthalensis*	0.044	57.3	Classical calibration
Shanidar IV	*Homo neanderthalensis*	0.044	48.9	Inverse calibration
Shanidar V	*Homo neanderthalensis*	0.044	54.7	Classical calibration
Shanidar VI	*Homo neanderthalensis*	0.044	41.3	Classical calibration
Hortus 34	*Homo neanderthalensis*	0.04	48.8	Inverse calibration
St. Germaine la Rive	*Homo sapiens*	0.04	45.1	Inverse calibration
Tagliente I	*Homo sapiens*	0.04	51.2	Classical calibration
Veryier	*Homo sapiens*	0.04	45.1	Inverse calibration
La Ferrassie 1	*Homo neanderthalensis*	0.038	58.7	Inverse calibration
La Ferrassie 2	*Homo neanderthalensis*	0.038	50.8	Inverse calibration
Spy 2	*Homo neanderthalensis*	0.036	55.5	Inverse calibration
Baousso de Torre I	*Homo sapiens*	0.03	76.3	Classical calibration

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Table 3.4 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Baousso de Torre II	*Homo sapiens*	0.03	68.4	Classical calibration
Barma Grande V	*Homo sapiens*	0.03	66.1	Classical calibration
Cro Magnon 1	*Homo sapiens*	0.03	64.7	Inverse calibration
Cro Magnon 3	*Homo sapiens*	0.03	63.7	Classical calibration
Grotte des Enfants V	*Homo sapiens*	0.03	51.8	Classical calibration
La Rochette 1	*Homo sapiens*	0.03	50.4	Inverse calibration
Paglicci I	*Homo sapiens*	0.03	59.1	Inverse calibration
Paviland I	*Homo sapiens*	0.03	56.0	Inverse calibration
Predmost III	*Homo sapiens*	0.03	63.2	Inverse calibration
Predmost IV	*Homo sapiens*	0.03	51.2	Inverse calibration
Predmost IX	*Homo sapiens*	0.03	46.5	Inverse calibration
Predmost X	*Homo sapiens*	0.03	48.0	Inverse calibration
Predmost XIV	*Homo sapiens*	0.03	51.3	Inverse calibration
San Teodoro 4	*Homo sapiens*	0.03	54.4	Inverse calibration
Willendorf 1	*Homo sapiens*	0.03	45.5	Inverse calibration
Brno 2	*Homo neanderthalensis*	0.024	58.4	Inverse calibration
Cap Blanc I	*Homo sapiens*	0.021	41.3	Inverse calibration
Pataud 10	*Homo sapiens*	0.021	52.9	Inverse calibration
Bruniquel XXIV	*Homo sapiens*	0.02	46.4	Classical calibration
Caviglione I	*Homo sapiens*	0.02	60.1	Classical calibration
Font de foret I	*Homo neanderthalensis*	0.02	62.0	Inverse calibration
La Madelaine	*Homo sapiens*	0.02	51.7	Inverse calibration
Chancellade	*Homo sapiens*	0.017	50.7	Inverse calibration
Le Peyrat 5	*Homo sapiens*	0.017	54.6	Inverse calibration
Le Peyrat 6	*Homo sapiens*	0.017	42.6	Inverse calibration

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Table 3.4 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Obercassel I	*Homo sapiens*	0.015	47.3	Inverse calibration
Obercassel II	*Homo sapiens*	0.015	55.8	Inverse calibration
Sandalja I	*Homo sapiens*	0.0123	48.3	Inverse calibration
San Teodoro 1	*Homo sapiens*	0.01	60.6	Inverse calibration
Hotu 2	*Homo sapiens*	0.009	51.1	Inverse calibration
Hotu 3	*Homo sapiens*	0.009	43.2	Inverse calibration
Combe-Capelle 1	*Homo sapiens*	0.007	49.2	Inverse calibration
Culoz 1	*Homo sapiens*	0.007	49.7	Inverse calibration
Culoz 2	*Homo sapiens*	0.007	47.0	Inverse calibration
Gramat 1	*Homo sapiens*	0.007	54.7	Classical calibration
Montardit 3	*Homo sapiens*	0.007	**15.5**	Profile likelihood

Table 3.5: Final Body Mass Estimates, Purported Ancestors

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Stw 431	*Australopithecus africanus*	4.0	51.4	Inverse calibration
Sts 392	*Australopithecus africanus*	2.6	28.0	Classical calibration
Stw 25	*Australopithecus africanus*	2.6	29.5	Inverse calibration
Stw 443	*Australopithecus africanus*	2.6	36.5	Classical calibration
Stw 99	*Australopithecus africanus*	2.6	40.5	Classical calibration

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Table 3.5 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
KNM-ER 1475	*Homo sp.*	2.0	48.8	Inverse calibration
KNM-ER 3228	*Homo habilis*	2.0	58.0	Classical calibration
Dmanisi 4167	*Homo sp.*	1.7	46.6	Inverse calibration
Dmanisi 4507	*Homo sp.*	1.7	46.4	Classical calibration
KNM-ER 1808	*Homo erectus*	1.7	63.7	Classical calibration
KNM-ER 736	*Homo sp.*	1.7	60.6	Inverse calibration
KNM-ER 737	*Homo sp.*	1.6	54.2	Inverse calibration
KNM-ER 15000	*Homo erectus*	1.6	54.2	Inverse calibration
OH 34	*Homo erectus*	1.0	51.4	Inverse calibration
Trinil I	*Homo erectus*	1.0	54.9	Inverse calibration
Trinil II	*Homo erectus*	1.0	67.4	Classical calibration
OH 28	*Homo erectus*	0.7	56.8	Inverse calibration
Peking IV	*Homo erectus*	0.04	46.0	Classical calibration
Broken Hill E691	*Homo sapiens*	0.3	68.6	Inverse calibration
Solo (Ngandong)	*Homo erectus*	0.2	50.6	Classical calibration
Ehringsdorf 5	*Homo neanderthalensis*	0.15	60.8	Inverse calibration
Krapina II	*Homo neanderthalensis*	0.1	51.3	Classical calibration
Qafzeh IX	*Homo sapiens*	0.1	59.8	Classical calibration
Skhul III	*Homo sapiens*	0.1	64.7	Inverse calibration
Skhul IV	*Homo sapiens*	0.1	52.5	Inverse calibration
Skhul VI	*Homo sapiens*	0.1	54.4	Inverse calibration
Skhul VII	*Homo sapiens*	0.1	48.8	Inverse calibration
Tabun C1	*Homo neanderthalensis*	0.075	48.3	Inverse calibration

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Table 3.5 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Tabun E1	*Homo neanderthalensis*	0.075	51.4	Inverse calibration
Sedia-del-Diavolo	*Homo neanderthalensis*	0.07	57.8	Inverse calibration
Biscegli I	*Homo neanderthalensis*	0.064	56.4	Inverse calibration
Kebarah M1	*Homo sapiens*	0.06	45.1	Inverse calibration
Kebarah M7	*Homo sapiens*	0.06	44.0	Inverse calibration
Kebarah P14	*Homo sapiens*	0.06	50.4	Inverse calibration
Kebarah P20	*Homo sapiens*	0.06	48.6	Inverse calibration
Kebarah P24	*Homo sapiens*	0.06	59.1	Inverse calibration
Kebarah P9	*Homo sapiens*	0.06	46.6	Inverse calibration
Neanderthal I	*Homo neanderthalensis*	0.055	55.4	Inverse calibration
Amud I	*Homo neanderthalensis*	0.054	67.1	Inverse calibration
La Chapelle	*Homo sapiens*	0.05	56.2	Inverse calibration
La Quina 5	*Homo neanderthalensis*	0.05	55.7	Inverse calibration
Shanidar I	*Homo neanderthalensis*	0.044	57.3	Classical calibration
Shanidar IV	*Homo neanderthalensis*	0.044	48.9	Inverse calibration
Shanidar V	*Homo neanderthalensis*	0.044	54.7	Classical calibration
Shanidar VI	*Homo neanderthalensis*	0.044	41.3	Classical calibration

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Table 3.5 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Hortus 34	*Homo neanderthalensis*	0.04	48.8	Inverse calibration
St. Germaine la Rive	*Homo sapiens*	0.04	45.1	Inverse calibration
Tagliente I	*Homo sapiens*	0.04	51.2	Classical calibration
Veryier	*Homo sapiens*	0.04	45.1	Inverse calibration
La Ferrassie 1	*Homo neanderthalensis*	0.038	58.7	Inverse calibration
La Ferrassie 2	*Homo neanderthalensis*	0.038	50.8	Inverse calibration
Spy 2	*Homo neanderthalensis*	0.036	55.5	Inverse calibration
Baousso de Torre I	*Homo sapiens*	0.03	76.3	Classical calibration
Baousso de Torre II	*Homo sapiens*	0.03	68.4	Classical calibration
Barma Grande V	*Homo sapiens*	0.03	66.1	Classical calibration
Cro Magnon 1	*Homo sapiens*	0.03	64.7	Inverse calibration
Cro Magnon 3	*Homo sapiens*	0.03	63.7	Classical calibration
Grotte des Enfants V	*Homo sapiens*	0.03	51.8	Classical calibration
La Rochette 1	*Homo sapiens*	0.03	50.4	Inverse calibration
Paglicci I	*Homo sapiens*	0.03	59.1	Inverse calibration
Paviland I	*Homo sapiens*	0.03	56.0	Inverse calibration
Predmost III	*Homo sapiens*	0.03	63.2	Inverse calibration
Predmost IV	*Homo sapiens*	0.03	51.2	Inverse calibration
Predmost IX	*Homo sapiens*	0.03	46.5	Inverse calibration
Predmost X	*Homo sapiens*	0.03	48.0	Inverse calibration
Predmost XIV	*Homo sapiens*	0.03	51.3	Inverse calibration
San Teodoro 4	*Homo sapiens*	0.03	54.4	Inverse calibration
Willendorf 1	*Homo sapiens*	0.03	45.5	Inverse calibration

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Table 3.5 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Final Body Mass Estimate (kg)**	**BME technique**
Brno 2	*Homo neanderthalensis*	0.024	58.4	Inverse calibration
Cap Blanc I	*Homo sapiens*	0.021	41.3	Inverse calibration
Pataud 10	*Homo sapiens*	0.021	52.9	Inverse calibration
Bruniquel XXIV	*Homo sapiens*	0.02	46.4	Classical calibration
Caviglione I	*Homo sapiens*	0.02	60.0	Classical calibration
Font de foret I	*Homo neanderthalensis*	0.02	62.0	Inverse calibration
La Madelaine	*Homo sapiens*	0.02	51.7	Inverse calibration
Chancellade	*Homo sapiens*	0.017	50.7	Inverse calibration
Le Peyrat 5	*Homo sapiens*	0.017	54.6	Inverse calibration
Le Peyrat 6	*Homo sapiens*	0.017	42.6	Inverse calibration
Obercassel I	*Homo sapiens*	0.015	47.3	Inverse calibration
Obercassel II	*Homo sapiens*	0.015	55.8	Inverse calibration
Sandalja I	*Homo sapiens*	0.0123	48.3	Inverse calibration
San Teodoro 1	*Homo sapiens*	0.01	60.6	Inverse calibration
Hotu 2	*Homo sapiens*	0.009	51.1	Inverse calibration
Hotu 3	*Homo sapiens*	0.009	43.2	Inverse calibration
Combe-Capelle 1	*Homo sapiens*	0.007	49.2	Inverse calibration
Culoz 1	*Homo sapiens*	0.007	49.7	Inverse calibration
Culoz 2	*Homo sapiens*	0.007	47.0	Inverse calibration
Gramat 1	*Homo sapiens*	0.007	54.7	Classical calibration

3.2.2 Endocranial Volumes

Most research involving estimates of EV merely relies on previously published volumes. For specimens with only one estimate, the methods will be validated from the original article, but otherwise that point estimate will be used. Measurement error is inevitable in the assessment of endocranial volume, regardless of species.

Measures of endocasts (or any skeletal element) will never be exact and that should not be the expectation, but this type of error should be acknowledged.

There are several methods for estimating EV from fossil crania, and because fossil crania (particularly older material) are rarely complete most methods require some reconstruction. Reconstructions are sometimes based on similar, more complete specimens, but sometimes are based essentially on the paleoanthropologist's eye for what looks correct (De Miguel and Henneberg, 2001). After reconstruction, estimates are made by water displacement (endocast), filling the cranium with a substance (e.g., seeds, shot) and then measuring the volume of that substance, or by CT scan of a virtual endocast. Virtual endocasts are thus far only available for *Australopithecus africanus* but offer a promising future of more accurate estimation of endocranial volume (Neubauer et al., 2012).

For most analyses, the full data set was used as were three subsets of that data. These are found in Tables 3.6, 3.7, 3.8. The fourth data subset is the same as Table 3.8 but with Neanderthals excluded.

Table 3.6: Fossil Dates and Estimated Cranial Volumes
(Entire Sample)

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
AL 162-28	*Australopithecus afarensis*	3.20	400	Blumenberg (1985)
AL 333-105	*Australopithecus afarensis*	3.20	352	Falk (1987)
AL 333-45	*Australopithecus afarensis*	3.20	500	Blumenberg (1985)
AL 288-1 (Lucy)	*Australopithecus afarensis*	3.10	410	Conroy (1997)
AL 444-2	*Australopithecus afarensis*	2.95	500	Wolpoff (1996)
MLD-1	*Australopithecus africanus*	2.90	500	Holloway (1973)

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Table 3.6 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
MLD-3	*Australopithecus africanus*	2.90	387	Wolpoff (1996)
MLD-37/38	*Australopithecus africanus*	2.90	435	Beals et al. (1984)
Stw 505 (Mr. Ples)	*Australopithecus africanus*	2.50	515	Conroy et al. (1998)
KNM WT 17000 (black skull)	*Paranthropus aethiopicus*	2.50	410	Conroy (1997)
Pleisianthropus type 2	*Australopithecus africanus*	2.50	457	Holloway et al. (2004b)
Sts 60	*Australopithecus africanus*	2.50	428	Blumenberg (1984)
Sts 5	*Australopithecus africanus*	2.50	485	Blumenberg (1984)
Sts 71	*Australopithecus africanus*	2.50	428	Conroy et al. (1990)
Sts 19/58	*Australopithecus africanus*	2.50	436	Blumenberg (1984)
Sts 17	*Australopithecus africanus*	2.50	425	Wolpoff (1996)
Sts 25	*Australopithecus africanus*	2.50	375	Wolpoff (1996)
BOU-VP 12/130	*Australopithecus garhi*	2.50	450	Asfaw et al. (1999)
Omo L 323-1976-896	*Paranthropus boisei*	2.25	490	Brown et al. (1993)
KNM-ER 13750	*Paranthropus boisei*	2.00	500	Brown et al. (1993)

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Table 3.6 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
TM 1511	*Australopithecus africanus*	2.00	450	Wolpoff (1996)
TM 1517	*Paranthropus robustus*	2.0	650	Day (1986)
MH1	*Australopithecus sediba*	1.96	420	Berger et al. (2010)
KNM-ER 23000	*Paranthropus boisei*	1.90	491	Wolpoff (1996)
SK 46	*Paranthropus robustus*	1.90	625	Wolpoff (1996)
SK 48	*Paranthropus robustus*	1.90	450	Wolpoff (1996)
SK 27	*Homo* ?	1.90	475	Wolpoff (1996)
SK 49	*Paranthropus robustus*	1.90	475	Wolpoff (1996)
SK 52	*Paranthropus robustus*	1.90	575	Wolpoff (1996)
SK 54	*Paranthropus robustus*	1.90	450	Wolpoff (1996)
SK 80	*Homo sp.*	1.90	475	Wolpoff (1996)
SK 1585	*Paranthropus robustus*	1.90	530	Wolpoff (1996)
SK 847	*Homo habilis*	1.90	554	Thackeray and Monteith (1997)
SK 80/847	*Homo habilis*	1.90	500	Wolpoff (1996)
Stw 53	early *Homo sp.*	1.90	570	De Miguel and Henneberg (2001)
Omo L894-1	*Homo sp.*	1.89	500	Wolpoff (1996)
KNM-ER 1470	*Homo rudolfensis*	1.89	775	Walker and Leakey (1978)
KNM-ER 1830	*Homo habilis*	1.89	500	Wolpoff (1996)
KNM-ER 3732	*Homo habilis*	1.89	700	Stringer (1986)
KNM-ER1805	*Homo habilis*	1.85	582	Wolpoff (1996)

Continued on next page

Table 3.6 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
Dmanisi A	*Homo sp.*	1.80	775	Gabunia et al. (2000)
Dmanisi B	*Homo sp.*	1.80	650	Gabunia et al. (2000)
OH 24	*Homo habilis*	1.80	590	Blumenberg (1984)
KNM-WT 17400	*Paranthropus boisei*	1.80	500	Brown et al. (1993)
KNM-ER 3733	*Homo erectus*	1.78	848	Wolpoff (1996)
OH 5	*Paranthropus boisei*	1.77	530	Blumenberg (1985)
Sangiran 31	*Homo erectus*	1.66	1000	Conroy (1997)
KNM-ER 406	*Paranthropus boisei*	1.64	510	Blumenberg (1984)
KNM-ER 407	*Paranthropus boisei*	1.64	506	Falk and Kasinga (1983)
KNM-ER 732	*Paranthropus boisei*	1.64	500	Blumenberg (1985)
KNM-WT 15000	*Homo erectus*	1.60	909	Begun and Walker (1993)
KNM-ER 3883	*Homo erectus*	1.57	804	Conroy (1997)
Chesowanja 1	*Paranthropus boisei*	1.55	550	Beals et al. (1984)
KGA10-525	*Paranthropus boisei*	1.42	545	Suwa et al. (1997)
OH 9 (Chellean man)	*Homo erectus*	1.20	1067	Blumenberg (1984)
Sangiran 9	*Homo erectus*	1.20	856	Conroy (1997)
Gongwangling 1	*Homo erectus*	1.15	775	Conroy (1997)
Sangiran 4	*Homo erectus*	1.00	908	Conroy (1997)
Trinil 2	*Homo erectus*	1.00	940	Conroy (1997)
Sangiran 2	*Homo erectus*	0.90	900	Day (1986)
Sangiran 12	*Homo erectus*	0.90	900	Tobias (1971)
Sangiran 17	*Homo erectus*	0.90	1004	Conroy (1997)

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Table 3.6 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
Sangiran 10	*Homo erectus*	0.85	855	Blumenberg (1985)
OH12	*Homo erectus*	0.84	727	Blumenberg (1984)
Ternifine	*Homo erectus*	0.75	1300	Wolpoff (1996)
Ceprano	*Homo erectus*	0.70	1185	Helmuth (1999)
Bodo	*Homo sapiens*	0.60	1250	Conroy et al. (2000)
Sambungmacan 1	*Homo erectus*	0.50	1035	Leigh (1992a)
Arago 21	*Homo neanderthalensis*	0.40	1100	Conroy (1997)
Salé	*Homo sapiens*	0.40	880	Conroy (1997)
Zhoukoudian D1	*Homo erectus*	0.40	1030	Blumenberg (1984)
Zhoukoudian H3	*Homo erectus*	0.40	1140	Conroy (1997)
Zhoukoudian L1	*Homo erectus*	0.40	1225	Blumenberg (1984)
Zhoukoudian L2	*Homo erectus*	0.40	1015	Conroy (1997)
Zhoukoudian L3	*Homo erectus*	0.40	1030	Conroy (1997)
Ndutu 1	Archaic *Homo sapiens*	0.35	1100	Blumenberg (1984)
Saldanha 1	*Homo sapiens*	0.35	1225	Blumenberg (1984)
Yunxian	*Homo erectus*	0.35	1100	Wu and Poirier (1995)
Broken Hill 1 (Kabwe)	*Homo sapiens*	0.30	1280	Blumenberg (1984)
Atapuerca 4	*Homo sp.*	0.30	1390	Conroy (1997)
Atapuerca 5	*Homo sp.*	0.30	1125	Conroy (1997)
Petralona 1	*Homo neanderthalensis*	0.30	1220	Blumenberg (1984)
Reilingen	*Homo neanderthalensis*	0.30	1434	Helmuth (1999)

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Table 3.6 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
Steinheim 1	*Homo neanderthalensis*	0.30	1100	Blumenberg (1984)
Swanscombe 1	*Homo neanderthalensis*	0.30	1325	Blumenberg (1984)
Zhoukoudian IV	*Homo erectus*	0.30	850	Conroy (1997)
Narmada 1	Archaic *Homo sapiens*	0.30	1260	Ruff et al. (1997)
KNM-ER 3884	*Homo erectus*	0.27	1400	Bräuer et al. (1997)
Hexian	*Homo erectus*	0.25	1000	Conroy (1997)
Hexian 1	*Homo erectus*	0.25	1025	Conroy (1997)
Dali 1	Archaic *Homo erectus*	0.20	1120	Conroy (1997)
Solo 1/Ngandong 1	*Homo erectus*	0.20	1172	Conroy (1997)
Solo 5/Ngandong 5	*Homo erectus*	0.20	1251	Conroy (1997)
Solo 6/Ngandong 6	*Homo erectus*	0.20	1013	Conroy (1997)
Solo 9/Ngandong 9	*Homo erectus*	0.20	1135	Blumenberg (1984)
Solo 10/Ngandong 10	*Homo erectus*	0.20	1231	Conroy (1997)
Sambungmacan 3	*Homo erectus*	0.20	900	Broadfield et al. (2001)
Jinniushan	Archaic *Homo sapiens*	0.187	1300	Conroy (1997)
Vértesszöllös 2	Archaic *Homo sapiens*	0.186	1300	Conroy (1997)
Biache	*Homo neanderthalensis*	0.178	1200	Conroy (1997)
Fontéchevade 2	*Homo neanderthalensis*	0.16	1350	Wolpoff (1996)
Ehringsdorf	*Homo neanderthalensis*	0.15	1450	Wolpoff (1996)

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Table 3.6 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
Suard 1, LaChaise	*Homo neanderthalensis*	0.15	1065	Wolpoff (1996)
Florisbad 1	Archaic *Homo sapiens*	0.15	1280	Blumenberg (1984)
Krapina D	*Homo neanderthalensis*	0.13	1450	Phenice and Sauer (1977)
Krapina 3C	*Homo neanderthalensis*	0.13	1200	Phenice and Sauer (1977)
Omo 1	*Homo sapiens*	0.13	1400	Wolpoff (1996)
Omo 2	*Homo sapiens*	0.13	1200	Blumenberg (1984)
Laetoli 18	*Homo sapiens*	0.125	1200	Blumenberg (1984)
Jebel Irhoud 1	*Homo sapiens*	0.10	1305	Wolpoff (1996)
Jebel Irhoud 2	*Homo sapiens*	0.10	1305	Helmuth (1999)
Lijiang	*Homo sapiens*	0.10	1300	Wu and Poirier (1995)
Saccopastore 1	*Homo neanderthalensis*	0.10	1245	Wolpoff (1996)
Saccopastore 2	*Homo neanderthalensis*	0.10	1300	Wolpoff (1996)
Qafzeh 11	*Homo sapiens*	0.093	1280	Ruff et al. (1997)
Qafzeh 6	*Homo sapiens*	0.093	1568	Helmuth (1999)
Qafzeh 9	*Homo sapiens*	0.093	1531	Wolpoff (1996)
Skhul 2	*Homo sapiens*	0.09	1300	Coon (1962)
Skhul 4	*Homo sapiens*	0.09	1554	Helmuth (1999)
Skhul 5	*Homo sapiens*	0.09	1520	Helmuth (1999)
Skhul 9	*Homo sapiens*	0.09	1585	Helmuth (1999)

Continued on next page

Table 3.6 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
Tabun C1	*Homo neanderthalensis*	0.075	1271	Wolpoff (1996)
Border Cave 1	*Homo sapiens*	0.072	1450	Helmuth (1999)
Liujiang	*Homo sapiens*	0.067	1480	Wu and Poirier (1995)
Gibralter 1	*Homo neanderthalensis*	0.06	1200	Helmuth (1999)
Monte Circero 1	*Homo neanderthalensis*	0.055	1552	Helmuth (1999)
Neanderthal 1	*Homo neanderthalensis*	0.055	1450	Phenice and Sauer (1977)
Amud 1	*Homo neanderthalensis*	0.054	1740	Helmuth (1999)
Ganovce 1	*Homo neanderthalensis*	0.05	1320	Ruff et al. (1997)
La Chapelle Aux Saints	*Homo neanderthalensis*	0.05	1625	Wolpoff (1996)
La Quina 5	*Homo neanderthalensis*	0.05	1350	Ruff et al. (1997)
Shanidar 1	*Homo neanderthalensis*	0.044	1600	Phenice and Sauer (1977)
Shanidar 5	*Homo neanderthalensis*	0.044	1550	Ruff et al. (1997)
Galilee	*Homo neanderthalensis*	0.04	1400	Von Bonin (1963)

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Table 3.6 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
Le Moustier 1	*Homo neanderthalensis*	0.04	1352	Helmuth (1999)
Saint Germain-la-Riviere 1	*Homo sapiens*	0.04	1354	Ruff et al. (1997)
La Ferrassie 1	*Homo neanderthalensis*	0.038	1641	Phenice and Sauer (1977)
Spy 1	*Homo neanderthalensis*	0.036	1525	Helmuth (1999)
Spy 2	*Homo neanderthalensis*	0.036	1553	Ruff et al. (1997)
Eyasi	*Homo sapiens*	0.035	1235	Conroy (1997)
Mladeč 5	*Homo sapiens*	0.035	1650	Wolpoff (1996)
Nazlet Khater 1	*Homo sapiens*	0.033	1420	Ruff et al. (1997)
Cro-Magnon 1	*Homo sapiens*	0.03	1636	Wolpoff (1996)
Cro-Magnon 2	*Homo sapiens*	0.03	1402	Helmuth (1999)
Cro-Magnon 3	*Homo sapiens*	0.03	1730	Wolpoff (1996)
Predmosti 10	*Homo sapiens*	0.03	1452	Helmuth (1999)
Predmosti 3	*Homo sapiens*	0.03	1580	Helmuth (1999)
Predmosti 4	*Homo sapiens*	0.03	1518	Ruff et al. (1997)
Predmosti 9	*Homo sapiens*	0.03	1555	Ruff et al. (1997)
Barma Grande 2	*Homo sapiens*	0.03	1748	Helmuth (1999)
Grimaldi 4	*Homo sapiens*	0.028	1715	Helmuth (1999)
Grimaldi 5	*Homo sapiens*	0.028	1375	Helmuth (1999)
Paderbourne	*Homo sapiens*	0.027	1531	Ruff et al. (1997)
Zhoukoudian 101	*Homo sapiens*	0.027	1500	Helmuth (1999)
Zhoukoudian 102	*Homo sapiens*	0.027	1380	Helmuth (1999)

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Table 3.6 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
Zhoukoudian 103	*Homo sapiens*	0.027	1300	Helmuth (1999)
Dolni Vestonice 3	*Homo sapiens*	0.026	1293	Helmuth (1999)
Pavlov 1	*Homo sapiens*	0.026	1522	Ruff et al. (1997)
Pataud 1	*Homo sapiens*	0.021	1380	Ruff et al. (1997)
Boskop	*Homo sapiens*	0.02	1650	Tobias (1971)
Arene Candide	*Homo sapiens*	0.019	1490	Ruff et al. (1997)
Minatogawa 1	*Homo sapiens*	0.018	1390	Ruff et al. (1997)
Minatogawa 2	*Homo sapiens*	0.018	1170	Ruff et al. (1997)
Minatogawa 4	*Homo sapiens*	0.018	1090	Ruff et al. (1997)
Brno 1	*Homo sapiens*	0.018	1600	Helmuth (1999)
Brno 2	*Homo sapiens*	0.018	1543	Helmuth (1999)
Chancelade 1	*Homo sapiens*	0.017	1700	Ruff et al. (1997)
Cape Flats	*Homo sapiens*	0.016	1230	Helmuth (1999)
Tuinplass (Springbok)	*Homo sapiens*	0.015	1540	Helmuth (1999)
Wadjak 1	*Homo sapiens*	0.015	1550	Helmuth (1999)
Wadjak 2	*Homo sapiens*	0.015	1650	Helmuth (1999)
WLH 50	*Homo sapiens*	0.015	1540	Brown (2000)
Fish Hoek	*Homo sapiens*	0.014	1600	Helmuth (1999)
Keilor	*Homo sapiens*	0.013	1593	Helmuth (1999)
Bruniquel 2	*Homo sapiens*	0.012	1555	Ruff et al. (1997)
Cap Blanc 1	*Homo sapiens*	0.012	1434	Ruff et al. (1997)
Oberkassel 1	*Homo sapiens*	0.012	1500	Ruff et al. (1997)
Oberkassel 2	*Homo sapiens*	0.012	1370	Ruff et al. (1997)
Talgai 1	*Homo sapiens*	0.012	1370	Helmuth (1999)
San Teodoro 7	*Homo sapiens*	0.012	1500	Aimar and Giacobini (1989)

Continued on next page

Table 3.6 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
San Teodoro 1	*Homo sapiens*	0.01	1565	Ruff et al. (1997)
San Teodoro 2	*Homo sapiens*	0.011	1569	Ruff et al. (1997)
San Teodoro 3	*Homo sapiens*	0.011	1560	Ruff et al. (1997)
San Teodoro 5	*Homo sapiens*	0.011	1484	Ruff et al. (1997)
Arene Candide 1	*Homo sapiens*	0.011	1414	Ruff et al. (1997)
Arene Candide 2	*Homo sapiens*	0.011	1424	Ruff et al. (1997)
Arene Candide 4	*Homo sapiens*	0.011	1520	Ruff et al. (1997)
Arene Candide 5	*Homo sapiens*	0.011	1661	Ruff et al. (1997)
Veryier 1	*Homo sapiens*	0.01	1430	Ruff et al. (1997)
Cohuna	*Homo sapiens*	0.01	1260	Helmuth (1999)
Gamble's Cave	*Homo sapiens*	0.01	1500	Helmuth (1999)
Gamble's Cave 4	*Homo sapiens*	0.01	1470	Tobias (1971)
Gamble's Cave 5	*Homo sapiens*	0.01	1530	Tobias (1971)
Tepexpan	*Homo sapiens*	0.01	1540	Phenice and Sauer (1977)
Tze-Yang	*Homo sapiens*	0.01	1210	Phenice and Sauer (1977)
Combe Capelle	*Homo sapiens*	0.007	1522	Helmuth (1999)

Table 3.7: Fossil Dates and Estimated Cranial Volumes—1.9 mya to present

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
SK 80	*Homo sp.*	1.9	475	Wolpoff (1996)
SK 847	*Homo habilis*	1.9	554	Thackeray and Monteith (1997)
SK 80/847	*Homo habilis*	1.9	500	Wolpoff (1996)
Stw 53	*Homo habilis*	1.9	570	De Miguel and Henneberg (2001)
Omo L894-1	*Homo sp.*	1.89	500	Wolpoff (1996)
KNM-ER 1470	*Homo rudolfensis*	1.89	775	Walker and Leakey (1978)
KNM-ER 1830	*Homo habilis*	1.89	500	Wolpoff (1996)
KNM-ER 3732	*Homo habilis*	1.89	700	Stringer (1986)
KNM-ER 1805	*Homo habilis*	1.85	582	Wolpoff (1996)
Dmanisi A	*Homo sp.*	1.8	775	Gabunia et al. (2000)
Dmanisi B	*Homo sp.*	1.8	650	Gabunia et al. (2000)
OH 24	*Homo habilis*	1.8	590	Blumenberg (1984)
KNM-ER 3733	*Homo erectus*	1.7	848	Wolpoff (1996)
Sangiran 31	*Homo erectus*	1.66	1000	Conroy (1997)
KNM-WT 15000	*Homo erectus*	1.6	909	Begun and Walker (1993)
KNM-ER 3883	*Homo erectus*	1.57	804	Conroy (1997)
OH9	*Homo erectus*	1.2	1067	Blumenberg (1984)
Sangiran 9	*Homo erectus*	1.2	856	Conroy (1997)

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Table 3.7 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Endocranial Volume Estimates**
Gongwangling 1	*Homo erectus*	1.15	775	Conroy (1997)
Sangiran 4	*Homo erectus*	1.0	908	Conroy (1997)
Trinil 2	*Homo erectus*	0.9	940	Conroy (1997)
Sangiran 2	*Homo erectus*	0.9	900	Day (1986)
Sangiran 12	*Homo erectus*	0.9	900	Tobias (1971)
Sangiran 17	*Homo erectus*	0.9	900	Conroy (1997)
Sangiran 10	*Homo erectus*	0.85	855	Blumenberg (1985)
OH 12	*Homo erectus*	0.84	727	Blumenberg (1984)
Ternifine	*Homo erectus*	0.75	1300	Wolpoff (1996)
Ceprano	*Homo erectus*	0.7	1185	Helmuth (1999)
Bodo	*Homo sapiens*	0.6	1300	Conroy et al. (2000)
Sambungmacan 1	*Homo erectus*	0.5	1035	Leigh (1992a)
Arago 21	*Homo neanderthalensis*	0.4	1100	Conroy (1997)
Salé	*Homo sapiens*	0.4	880	Conroy (1997)
Zhoukoudian D1	*Homo erectus*	0.4	1030	Blumenberg (1984)
Zhoukoudian H3	*Homo erectus*	0.4	1140	Conroy (1997)
Zhoukoudian L1	*Homo erectus*	0.4	1225	Blumenberg (1984)
Zhoukoudian L2	*Homo erectus*	0.4	1015	Conroy (1997)
Zhoukoudian L3	*Homo erectus*	0.4	1030	Conroy (1997)
Ndutu 1	*Homo sapiens*	0.35	1100	Blumenberg (1984)
Saldanha 1 (Elandsfontein)	*Homo sapiens*	0.35	1225	Blumenberg (1984)
Yunxian	*Homo erectus*	0.35	1100	Wu and Poirier (1995)
Atapuerca 4	*Homo sp.*	0.3	1390	Conroy (1997)

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Table 3.7 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Endocranial Volume Estimates**
Atapuerca 5	*Homo sp.*	0.3	1125	Conroy (1997)
Broken Hill (Kabwe)	*Homo sapiens*	0.3	1280	Blumenberg (1984)
Petralona 1	*Homo neanderthalensis*	0.3	1220	Blumenberg (1984)
Reilingen	*Homo neanderthalensis*	0.3	1434	Helmuth (1999)
Steinheim 1	*Homo neanderthalensis*	0.3	1100	Blumenberg (1984)
Swanscombe 1	*Homo neanderthalensis*	0.3	1325	Blumenberg (1984)
Zhoukoudian IV	*Homo erectus*	0.3	850	Conroy (1997)
Narmada	*Homo sp.*	0.3	1260	Ruff et al. (1997)
KNM-ER 3884	*Homo erectus*	0.27	1400	Bräuer et al. (1997)
Hexian	*Homo erectus*	0.25	1000	Conroy (1997)
Hexian 1	*Homo erectus*	0.25	1025	Conroy (1997)
Dali 1	*Homo erectus*	0.205	1120	Conroy (1997)
Ehringsdorf	*Homo neanderthalensis*	0.203	1450	Wolpoff (1996)
Solo/Ngandong 1	*Homo erectus*	0.2	1172	Conroy (1997)
Solo/Ngandong 5	*Homo erectus*	0.2	1251	Conroy (1997)
Solo/Ngandong 6	*Homo erectus*	0.2	1013	Conroy (1997)
Solo/Ngandong 9	*Homo erectus*	0.2	1135	Blumenberg (1984)
Solo/Ngandong 10	*Homo erectus*	0.2	1231	Conroy (1997)
Sambungmacan 3	*Homo erectus*	0.2	900	Broadfield et al. (2001)
Jinniushan	*Homo erectus*	0.187	1300	Conroy (1997)

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Table 3.7 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Endocranial Volume Estimates**
Vértesszöllös 2	*Homo neanderthalensis*	0.186	1300	Conroy (1997)
Biache	*Homo neanderthalensis*	0.178	1200	Conroy (1997)
Fontéchevade 2	*Homo neanderthalensis*	0.16	1350	Wolpoff (1996)
Suard 1, LaChaise	*Homo neanderthalensis*	0.151	1065	Wolpoff (1996)
Florisbad 1	*Homo sapiens*	0.15	1280	Blumenberg (1984)
Krapina D	*Homo neanderthalensis*	0.13	1280	Phenice and Sauer (1977)
Krapina 3 C	*Homo neanderthalensis*	0.13	1200	Phenice and Sauer (1977)
Omo 1	*Homo sapiens*	0.13	1400	Wolpoff (1996)
Omo 2	*Homo sapiens*	0.13	1200	Blumenberg (1984)
Laetoli 18	*Homo sapiens*	0.125	1200	Blumenberg (1984)
Jebel Irhoud 1	*Homo sapiens*	0.1	1305	Wolpoff (1996)
Jebel Irhoud 2	*Homo sapiens*	0.1	1305	Helmuth (1999)
Lijiang	*Homo sapiens*	0.1	1300	Wu and Poirier (1995)
Saccopastore 1	*Homo neanderthalensis*	0.1	1245	Wolpoff (1996)
Saccopastore 2	*Homo neanderthalensis*	0.1	1300	Wolpoff (1996)
Tabun C1	*Homo neanderthalensis*	0.075	1271	Wolpoff (1996)

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Table 3.7 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Endocranial Volume Estimates**
Qafzeh 11	*Homo sapiens*	0.093	1280	Ruff et al. (1997)
Qafzeh 6	*Homo sapiens*	0.093	1531	Helmuth (1999)
Skhul 2	*Homo sapiens*	0.09	1300	Coon (1962)
Skhul 4	*Homo sapiens*	0.09	1554	Helmuth (1999)
Skhul 5	*Homo sapiens*	0.09	1520	Helmuth (1999)
Skhul 9	*Homo sapiens*	0.09	1585	Helmuth (1999)
Border Cave 1	*Homo sapiens*	0.072	1450	Helmuth (1999)
La Ferrassie 1	*Homo neanderthalensis*	0.038	1641	Phenice and Sauer (1977)
Liujiang	*Homo sapiens*	0.067	1480	Wu and Poirier (1995)
Gibralter 1	*Homo neanderthalensis*	0.06	1200	Helmuth (1999)
Monte Cicero 1	*Homo neanderthalensis*	0.055	1552	Helmuth (1999)
Amud 1	*Homo neanderthalensis*	0.054	1740	Helmuth (1999)
Neanderthal 1	*Homo neanderthalensis*	0.05	1450	Phenice and Sauer (1977)
Ganovce 1	*Homo neanderthalensis*	0.05	1450	Ruff et al. (1997)
La Chapelle aux Saints	*Homo neanderthalensis*	0.05	1450	Wolpoff (1996)
La Quina 5	*Homo neanderthalensis*	0.05	1350	Ruff et al. (1997)

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Table 3.7 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Endocranial Volume Estimates**
Shanidar 1	*Homo neanderthalensis*	0.044	1600	Phenice and Sauer (1977)
Shanidar 5	*Homo neanderthalensis*	0.044	1550	Ruff et al. (1997)
Galilee	*Homo neanderthalensis*	0.04	1400	Von Bonin (1963)
Le Moustier 1	*Homo neanderthalensis*	0.04	1352	Helmuth (1999)
Saint Germaine La Rive	*Homo sapiens*	0.04	1354	Ruff et al. (1997)
Spy 1	*Homo neanderthalensis*	0.036	1525	Helmuth (1999)
Spy 2	*Homo neanderthalensis*	0.036	1553	Ruff et al. (1997)
Eyasi	*Homo sapiens*	0.035	1235	Conroy (1997)
Mladeč	*Homo sapiens*	0.035	1650	Wolpoff (1996)
Nazlet Khater 1	*Homo sapiens*	0.033	1420	Ruff et al. (1997)
Cro-Magnon 1	*Homo sapiens*	0.03	1636	Wolpoff (1996)
Cro-Magnon 2	*Homo sapiens*	0.03	1402	Helmuth (1999)
Cro-Magnon 3	*Homo sapiens*	0.03	1730	Wolpoff (1996)
Predmosti 10	*Homo sapiens*	0.03	1452	Helmuth (1999)
Predmosti 3	*Homo sapiens*	0.03	1580	Helmuth (1999)
Predmosti 4	*Homo sapiens*	0.03	1518	Ruff et al. (1997)
Predmosti 9	*Homo sapiens*	0.03	1555	Ruff et al. (1997)
Grimaldi 4	*Homo sapiens*	0.028	1715	Helmuth (1999)
Grimaldi 5	*Homo sapiens*	0.028	1375	Helmuth (1999)

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Table 3.7 – continued from previous page

Fossil Specimen	Designation	Date (mya)	Endocranial Volume Estimates	Endocranial Volume Estimates
Paderbourne	*Homo sapiens*	0.027	1531	Ruff et al. (1997)
Zhoukoudian 101	*Homo sapiens*	0.027	1500	Helmuth (1999)
Zhoukoudian 102	*Homo sapiens*	0.027	1380	Helmuth (1999)
Zhoukoudian 103	*Homo sapiens*	0.027	1300	Helmuth (1999)
Dolni Vestonice 3	*Homo sapiens*	0.026	1293	Helmuth (1999)
Pavlov 1	*Homo sapiens*	0.026	1522	Ruff et al. (1997)
Pataud 1	*Homo sapiens*	0.021	1380	Ruff et al. (1997)
Boskop	*Homo sapiens*	0.02	1650	Tobias (1971)
Barma Grande 2	*Homo sapiens*	0.03	1748	Helmuth (1999)
Arene Candide	*Homo sapiens*	0.019	1490	Ruff et al. (1997)
Minatogawa 1	*Homo sapiens*	0.018	1390	Ruff et al. (1997)
Minatogawa 2	*Homo sapiens*	0.018	1170	Ruff et al. (1997)
Minatogawa 4	*Homo sapiens*	0.018	1090	Ruff et al. (1997)
Brno 1	*Homo sapiens*	0.018	1600	Helmuth (1999)
Brno 2	*Homo sapiens*	0.018	1543	Helmuth (1999)
Cape Flats	*Homo sapiens*	0.016	1230	Helmuth (1999)
Tuinplass (Springbok)	*Homo sapiens*	0.015	1230	Helmuth (1999)
Wadjak 1	*Homo sapiens*	0.015	1540	Helmuth (1999)
Wadjak 2	*Homo sapiens*	0.015	1650	Helmuth (1999)
WLH 50	*Homo sapiens*	0.015	1540	Brown (2000)
Fish Hoek 1	*Homo sapiens*	0.014	1600	Helmuth (1999)
Chancelade 1	*Homo sapiens*	0.017	1700	Ruff et al. (1997)
Keilor	*Homo sapiens*	0.013	1593	Helmuth (1999)
Bruniquel 2	*Homo sapiens*	0.012	1555	Ruff et al. (1997)
Cap Blanc 1	*Homo sapiens*	0.012	1434	Ruff et al. (1997)
Oberkassel 1	*Homo sapiens*	0.012	1500	Ruff et al. (1997)

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Table 3.7 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Endocranial Volume Estimates**
Oberkassel 2	*Homo sapiens*	0.012	1370	Ruff et al. (1997)
Talgai	*Homo sapiens*	0.012	1370	Helmuth (1999)
San Teodoro 7	*Homo sapiens*	0.012	1500	Aimar and Giacobini (1989)
San Teodoro 1	*Homo sapiens*	0.01	1565	Ruff et al. (1997)
San Teodoro 2	*Homo sapiens*	0.011	1569	Ruff et al. (1997)
San Teodoro 3	*Homo sapiens*	0.011	1560	Ruff et al. (1997)
San Teodoro 5	*Homo sapiens*	0.011	1484	Ruff et al. (1997)
Arene Candide 1	*Homo sapiens*	0.011	1414	Ruff et al. (1997)
Arene Candide 2	*Homo sapiens*	0.011	1424	Ruff et al. (1997)
Arene Candide 4	*Homo sapiens*	0.011	1520	Ruff et al. (1997)
Arene Candide 5	*Homo sapiens*	0.011	1661	Ruff et al. (1997)
Veryier 1	*Homo sapiens*	0.01	1430	Ruff et al. (1997)
Cohuna	*Homo sapiens*	0.01	1260	Helmuth (1999)
Gamble's Cave 4	*Homo sapiens*	0.01	1470	Tobias (1971)
Gamble's Cave 5	*Homo sapiens*	0.01	1530	Tobias (1971)
Tepexpan	*Homo sapiens*	0.01	1540	Phenice and Sauer (1977)
Tze-Yang	*Homo sapiens*	0.01	1210	Phenice and Sauer (1977)
Combe Capelle	*Homo sapiens*	0.007	1522	Helmuth (1999)

Table 3.8: Fossil Dates and Estimated Cranial Volumes for Purported "Ancestral" Australopithecines and All *Homo*

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
MLD-1	*Australopithecus africanus*	2.90	500	Holloway (1973)
MLD-3	*Australopithecus africanus*	2.90	387	Wolpoff (1996)
MLD-37/38	*Australopithecus africanus*	2.90	435	Beals et al. (1984)
Stw 505 (Mr. Ples)	*Australopithecus africanus*	2.50	515	Conroy et al. (1998)
Pleisianthropus type 2	*Australopithecus africanus*	2.50	457	Holloway et al. (2004b)
Sts 60	*Australopithecus africanus*	2.50	428	Blumenberg (1984)
Sts 5	*Australopithecus africanus*	2.50	485	Blumenberg (1984)
Sts 71	*Australopithecus africanus*	2.50	428	Conroy et al. (1990)
Sts 19/58	*Australopithecus africanus*	2.50	436	Blumenberg (1984)
Sts 17	*Australopithecus africanus*	2.50	425	Wolpoff (1996)
Sts 25	*Australopithecus africanus*	2.50	375	Wolpoff (1996)
TM 1511	*Australopithecus africanus*	2.00	450	Wolpoff (1996)
SK 27	*Homo* ?	1.90	475	Wolpoff (1996)

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Table 3.8 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
SK 80	*Homo sp.*	1.90	475	Wolpoff (1996)
SK 847	*Homo habilis*	1.90	554	Thackeray and Monteith (1997)
SK 80/847	*Homo habilis*	1.90	500	Wolpoff (1996)
Stw 53	early *Homo sp.*	1.90	570	De Miguel and Henneberg (2001)
Omo L894-1	*Homo sp.*	1.89	500	Wolpoff (1996)
KNM-ER 1470	*Homo rudolfensis*	1.89	775	Walker and Leakey (1978)
KNM-ER 1830	*Homo habilis*	1.89	500	Wolpoff (1996)
KNM-ER 3732	*Homo habilis*	1.89	700	Stringer (1986)
KNM-ER1805	*Homo habilis*	1.85	582	Wolpoff (1996)
Dmanisi A	*Homo sp.*	1.80	775	Gabunia et al. (2000)
Dmanisi B	*Homo sp.*	1.80	650	Gabunia et al. (2000)
OH 24	*Homo habilis*	1.80	590	Blumenberg (1984)
ER 3733	*Homo erectus*	1.78	848	Wolpoff (1996)
Sangiran 31	*Homo erectus*	1.66	1000	Conroy (1997)
KNM-WT 15000	*Homo erectus*	1.60	909	Begun and Walker (1993)
KNM-ER 3883	*Homo erectus*	1.57	804	Conroy (1997)
OH 9 (Chellean man)	*Homo erectus*	1.20	1067	Blumenberg (1984)
Sangiran 9	*Homo erectus*	1.20	856	Conroy (1997)
Gongwangling 1	*Homo erectus*	1.15	775	Conroy (1997)
Sangiran 4	*Homo erectus*	1.00	908	Conroy (1997)

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Table 3.8 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
Trinil 2	*Homo erectus*	1.00	940	Conroy (1997)
Sangiran 2	*Homo erectus*	0.90	900	Day (1986)
Sangiran 12	*Homo erectus*	0.90	900	Tobias (1971)
Sangiran 17	*Homo erectus*	0.90	1004	Conroy (1997)
Sangiran 10	*Homo erectus*	0.85	855	Blumenberg (1985)
OH12	*Homo erectus*	0.84	727	Blumenberg (1984)
Ternifine	*Homo erectus*	0.75	1300	Wolpoff (1996)
Ceprano	*Homo erectus*	0.70	1185	Helmuth (1999)
Bodo	*Homo sapiens*	0.60	1250	Conroy et al. (2000)
Sambungmacan 1	*Homo erectus*	0.50	1035	Leigh (1992a)
Arago 21	*Homo neanderthalensis*	0.40	1100	Conroy (1997)
Salé	*Homo sapiens*	0.40	880	Conroy (1997)
Zhoukoudian D1	*Homo erectus*	0.40	1030	Blumenberg (1984)
Zhoukoudian H3	*Homo erectus*	0.40	1140	Conroy (1997)
Zhoukoudian L1	*Homo erectus*	0.40	1225	Blumenberg (1984)
Zhoukoudian L2	*Homo erectus*	0.40	1015	Conroy (1997)
Zhoukoudian L3	*Homo erectus*	0.40	1030	Conroy (1997)
Ndutu 1	Archaic *Homo sapiens*	0.35	1100	Blumenberg (1984)
Saldanha 1	*Homo sapiens*	0.35	1225	Blumenberg (1984)
Yunxian	*Homo erectus*	0.35	1100	Wu and Poirier (1995)
Broken Hill 1 (Kabwe)	*Homo sapiens*	0.30	1280	Blumenberg (1984)
Atapuerca 4	*Homo sp.*	0.30	1390	Conroy (1997)
Atapuerca 5	*Homo sp.*	0.30	1125	Conroy (1997)

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Table 3.8 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
Petralona 1	*Homo neanderthalensis*	0.30	1220	Blumenberg (1984)
Reilingen	*Homo neanderthalensis*	0.30	1434	Helmuth (1999)
Steinheim 1	*Homo neanderthalensis*	0.30	1100	Blumenberg (1984)
Swanscombe 1	*Homo neanderthalensis*	0.30	1325	Blumenberg (1984)
Zhoukoudian IV	*Homo erectus*	0.30	850	Conroy (1997)
Narmada 1	Archaic *Homo sapiens*	0.30	1260	Ruff et al. (1997)
KNM-ER 3884	*Homo erectus*	0.27	1400	Bräuer et al. (1997)
Hexian	*Homo erectus*	0.25	1000	Conroy (1997)
Hexian 1	*Homo erectus*	0.25	1025	Conroy (1997)
Dali 1	Archaic *Homo erectus*	0.20	1120	Conroy (1997)
Solo 1/Ngandong 1	*Homo erectus*	0.20	1172	Conroy (1997)
Solo 5/Ngandong 5	*Homo erectus*	0.20	1251	Conroy (1997)
Solo 6/Ngandong 6	*Homo erectus*	0.20	1013	Conroy (1997)
Solo 9/Ngandong 9	*Homo erectus*	0.20	1135	Blumenberg (1984)
Solo 10/Ngandong 10	*Homo erectus*	0.20	1231	Conroy (1997)
Sambungmacan 3	*Homo erectus*	0.20	900	Broadfield et al. (2001)
Jinniushan	Archaic *Homo sapiens*	0.187	1300	Conroy (1997)
Vértesszöllös 2	Archaic *Homo sapiens*	0.186	1300	Conroy (1997)
Biache	*Homo neanderthalensis*	0.178	1200	Conroy (1997)

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Table 3.8 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
Fontéchevade 2	*Homo neanderthalensis*	0.16	1350	Wolpoff (1996)
Ehringsdorf	*Homo neanderthalensis*	0.15	1450	Wolpoff (1996)
Suard 1, LaChaise	*Homo neanderthalensis*	0.15	1065	Wolpoff (1996)
Florisbad 1	Archaic *Homo sapiens*	0.15	1280	Blumenberg (1984)
Krapina D	*Homo neanderthalensis*	0.13	1450	Phenice and Sauer (1977)
Krapina 3C	*Homo neanderthalensis*	0.13	1200	Phenice and Sauer (1977)
Omo 1	*Homo sapiens*	0.13	1400	Wolpoff (1996)
Omo 2	*Homo sapiens*	0.13	1200	Blumenberg (1984)
Laetoli 18	*Homo sapiens*	0.125	1200	Blumenberg (1984)
Jebel Irhoud 1	*Homo sapiens*	0.10	1305	Wolpoff (1996)
Jebel Irhoud 2	*Homo sapiens*	0.10	1305	Helmuth (1999)
Lijiang	*Homo sapiens*	0.10	1300	Wu and Poirier (1995)
Saccopastore 1	*Homo neanderthalensis*	0.10	1245	Wolpoff (1996)
Saccopastore 2	*Homo neanderthalensis*	0.10	1300	Wolpoff (1996)
Qafzeh 11	*Homo sapiens*	0.093	1280	Ruff et al. (1997)
Qafzeh 6	*Homo sapiens*	0.093	1568	Helmuth (1999)
Qafzeh 9	*Homo sapiens*	0.093	1531	Wolpoff (1996)
Skhul 2	*Homo sapiens*	0.09	1300	Coon (1962)

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Table 3.8 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
Skhul 4	*Homo sapiens*	0.09	1554	Helmuth (1999)
Skhul 5	*Homo sapiens*	0.09	1520	Helmuth (1999)
Skhul 9	*Homo sapiens*	0.09	1585	Helmuth (1999)
Tabun C1	*Homo neanderthalensis*	0.075	1271	Wolpoff (1996)
Border Cave 1	*Homo sapiens*	0.072	1450	Helmuth (1999)
Liujiang	*Homo sapiens*	0.067	1480	Wu and Poirier (1995)
Gibralter 1	*Homo neanderthalensis*	0.06	1200	Helmuth (1999)
Monte Circero 1	*Homo neanderthalensis*	0.055	1552	Helmuth (1999)
Neanderthal 1	*Homo neanderthalensis*	0.055	1450	Phenice and Sauer (1977)
Amud 1	*Homo neanderthalensis*	0.054	1740	Helmuth (1999)
Ganovce 1	*Homo neanderthalensis*	0.05	1320	Ruff et al. (1997)
La Chapelle Aux Saints	*Homo neanderthalensis*	0.05	1625	Wolpoff (1996)
La Quina 5	*Homo neanderthalensis*	0.05	1350	Ruff et al. (1997)
Shanidar 1	*Homo neanderthalensis*	0.044	1600	Phenice and Sauer (1977)
Shanidar 5	*Homo neanderthalensis*	0.044	1550	Ruff et al. (1997)

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Table 3.8 – continued from previous page

Fossil Specimen	**Designation**	**Date (mya)**	**Endocranial Volume Estimates**	**Source**
Galilee	*Homo neanderthalensis*	0.04	1400	Von Bonin (1963)
Le Moustier 1	*Homo neanderthalensis*	0.04	1352	Helmuth (1999)
Saint Germain-la-Riviere 1	*Homo sapiens*	0.04	1354	Ruff et al. (1997)
La Ferrassie 1	*Homo neanderthalensis*	0.038	1641	Phenice and Sauer (1977)
Spy 1	*Homo neanderthalensis*	0.036	1525	Helmuth (1999)
Spy 2	*Homo neanderthalensis*	0.036	1553	Ruff et al. (1997)
Eyasi	*Homo sapiens*	0.035	1235	Conroy (1997)
Mladeč 5	*Homo sapiens*	0.035	1650	Wolpoff (1996)
Nazlet Khater 1	*Homo sapiens*	0.033	1420	Ruff et al. (1997)
Cro-Magnon 1	*Homo sapiens*	0.03	1636	Wolpoff (1996)
Cro-Magnon 2	*Homo sapiens*	0.03	1402	Helmuth (1999)
Cro-Magnon 3	*Homo sapiens*	0.03	1730	Wolpoff (1996)
Predmosti 10	*Homo sapiens*	0.03	1452	Helmuth (1999)
Predmosti 3	*Homo sapiens*	0.03	1580	Helmuth (1999)
Predmosti 4	*Homo sapiens*	0.03	1518	Ruff et al. (1997)
Predmosti 9	*Homo sapiens*	0.03	1555	Ruff et al. (1997)
Barma Grande 2	*Homo sapiens*	0.03	1748	Helmuth (1999)
Grimaldi 4	*Homo sapiens*	0.028	1715	Helmuth (1999)
Grimaldi 5	*Homo sapiens*	0.028	1375	Helmuth (1999)
Paderbourne	*Homo sapiens*	0.027	1531	Ruff et al. (1997)

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Table 3.8 – continued from previous page

Fossil Specimen	Designation	Date (mya)	Endocranial Volume Estimates	Source
Zhoukoudian 101	*Homo sapiens*	0.027	1500	Helmuth (1999)
Zhoukoudian 102	*Homo sapiens*	0.027	1380	Helmuth (1999)
Zhoukoudian 103	*Homo sapiens*	0.027	1300	Helmuth (1999)
Dolni Vestonice 3	*Homo sapiens*	0.026	1293	Helmuth (1999)
Pavlov 1	*Homo sapiens*	0.026	1522	Ruff et al. (1997)
Pataud 1	*Homo sapiens*	0.021	1380	Ruff et al. (1997)
Boskop	*Homo sapiens*	0.02	1650	Tobias (1971)
Arene Candide	*Homo sapiens*	0.019	1490	Ruff et al. (1997)
Minatogawa 1	*Homo sapiens*	0.018	1390	Ruff et al. (1997)
Minatogawa 2	*Homo sapiens*	0.018	1170	Ruff et al. (1997)
Minatogawa 4	*Homo sapiens*	0.018	1090	Ruff et al. (1997)
Brno 1	*Homo sapiens*	0.018	1600	Helmuth (1999)
Brno 2	*Homo sapiens*	0.018	1543	Helmuth (1999)
Chancelade 1	*Homo sapiens*	0.017	1700	Ruff et al. (1997)
Cape Flats	*Homo sapiens*	0.016	1230	Helmuth (1999)
Tuinplass (Springbok)	*Homo sapiens*	0.015	1540	Helmuth (1999)
Wadjak 1	*Homo sapiens*	0.015	1550	Helmuth (1999)
Wadjak 2	*Homo sapiens*	0.015	1650	Helmuth (1999)
WLH 50	*Homo sapiens*	0.015	1540	Brown (2000)
Fish Hoek	*Homo sapiens*	0.014	1600	Helmuth (1999)
Keilor	*Homo sapiens*	0.013	1593	Helmuth (1999)
Bruniquel 2	*Homo sapiens*	0.012	1555	Ruff et al. (1997)
Cap Blanc 1	*Homo sapiens*	0.012	1434	Ruff et al. (1997)
Oberkassel 1	*Homo sapiens*	0.012	1500	Ruff et al. (1997)
Oberkassel 2	*Homo sapiens*	0.012	1370	Ruff et al. (1997)
Talgai 1	*Homo sapiens*	0.012	1370	Helmuth (1999)

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Table 3.8 – continued from previous page

Fossil Specimen	Designation	Date (mya)	Endocranial Volume Estimates	Source
San Teodoro 7	*Homo sapiens*	0.012	1500	Aimar and Giacobini (1989)
San Teodoro 1	*Homo sapiens*	0.01	1565	Ruff et al. (1997)
San Teodoro 2	*Homo sapiens*	0.011	1569	Ruff et al. (1997)
San Teodoro 3	*Homo sapiens*	0.011	1560	Ruff et al. (1997)
San Teodoro 5	*Homo sapiens*	0.011	1484	Ruff et al. (1997)
Arene Candide 1	*Homo sapiens*	0.011	1414	Ruff et al. (1997)
Arene Candide 2	*Homo sapiens*	0.011	1424	Ruff et al. (1997)
Arene Candide 4	*Homo sapiens*	0.011	1520	Ruff et al. (1997)
Arene Candide 5	*Homo sapiens*	0.011	1661	Ruff et al. (1997)
Veryier 1	*Homo sapiens*	0.01	1430	Ruff et al. (1997)
Cohuna	*Homo sapiens*	0.01	1260	Helmuth (1999)
Gamble's Cave	*Homo sapiens*	0.01	1500	Helmuth (1999)
Gamble's Cave 4	*Homo sapiens*	0.01	1470	Tobias (1971)
Gamble's Cave 5	*Homo sapiens*	0.01	1530	Tobias (1971)
Tepexpan	*Homo sapiens*	0.01	1540	Phenice and Sauer (1977)
Tze-Yang	*Homo sapiens*	0.01	1210	Phenice and Sauer (1977)
Combe Capelle	*Homo sapiens*	0.007	1522	Helmuth (1999)

3.2.3 Brain/Body Mass Relationships

Spearman's Rank Order Correlation

Spearman's rank-order correlation is a non-parametric measure of the correlation of two variables. These variables can be continuous or discrete; Spearman's can accommodate ordinal variables (hence "rank-order")

(Sokal and Rohlf, 1981). Some previous work has used Spearman's rank-order correlation to examine the temporal relationship between brain size and body mass by ordering each over time (Rightmire, 2004; Hawks, 2011). The computation of Spearman's rank-order is

$$r_2 = 1 - \frac{6 \sum d_i^2}{n(n^2 - 1)} \tag{3.1}$$

where d is the difference in ranks (x_i–y_i) and n is the sample size. This procedure is distinguished from Pearson's correlation because it examines the relationship between ranks. A perfect positive (1) or negative (-1) Spearman's correlation is not necessarily linear, as is required for a perfect positive or negative Pearson's correlation coefficient. A positive Spearman's coefficient means only that x_i increases as y_i increases; a negative Spearman's means that x_i decreases as y_i(Zar, 1998).

Hubert Test

The Hubert test is a non-parametric test that can incorporate a continuous variable over time described as a discrete variable (Konigsberg, 1990). Several studies of temporal trends in brain size or other cranial variables have employed it (Leigh, 1992a; Wood et al., 1994; Elton et al., 2001; Hawks, 2011). The Hubert test converts time estimates on a continuous scale into an ordinal rank variable. The dot product of these two vectors is then calculated for the observed data before the data is permuted and the dot product recalculated to form a null distribution. The Γ statistic, used to evaluate statistical significance, represents

$$(M + 1)/(N + 1) \tag{3.2}$$

where **M** is the number of permutations where the dot product is greater than or equal to the observed dot product and **N** is the number of permutations. The null hypothesis is no trend and is rejected if Γ is less than or equal to the significance level set by the analysis (usually 0.05).

Measurement error can be incorporated in the Hubert Test for any specimen that has multiple estimates. For specimens with "uncontroversial" estimates (relatively complete crania with estimates in agreement from multiple sources) a point estimate can be utilized. If there are multiple estimates (and therefore a distribution) a specimen mean and standard deviation can be used as parameters for simulation. An arbitrary number of random draws (e.g., 10,000 or 100,000) are made from a distribution with the mean and standard deviation of the specimen estimates. The resulting simulated distribution has its own mean and standard deviation, plus it will be normally distributed and independent of other specimens. Independence is a specific concern raised by Hawks because more complete endocasts are used to help reconstruct fragmentary

endocasts before EVs are estimated. The mean of this new, simulated distribution can be taken as the point estimate for that specimen.

Hawks (2011) allows for measurement error in his permuted data of the model-based Hubert test but not the observed data. He could have incorporated measurement error into the observed data through the same process as the expected data, just without permutation. If both sets of data are simulated with an arbitrary, but large, number of draws, then the overlap of the resulting distributions can be assessed for significance.

Fractional Polynomials

Before investigating the relationship of brain size to body mass over time, each variable must be separately modeled over geological time. Multivariate models of growth and allometry can differ depending on the type of curve chosen (e.g., logistic, Pütter, Gompertz) but many of these models have been criticized as overly complicated and inappropriate for somatic growth studies (Jolicoeur and Pirlot, 1988). One relatively recent approach to growth modelling is fractional polynomials (Royston and Altman, 1994; Sauerbrei et al., 2006). These polynomials are asymptotic and flexible because they are not limited to integers as exponents. The exponents can be integers (positive or negative), but they can also be fractions. In this study, the fractional polynomial regression will only include one variable (either brain size or body mass) dependent on geological time calculated as

$$Y = \sum_{i=1}^{n_p} \beta_{i=1} X^{p_1} \tag{3.3}$$

where Y is the response variable (either brain size or body mass), β is the regression coefficient, X is the predictor variable (geological time) and p is the exponent. The model is fit by a maximum likelihood procedure that compares a full model to reduced models. This procedure determines which p or ps from a set of numbers (e.g., -2, -1, $-1/2$, 0, $1/2$, 1, 2) provides the best-fit line. Modeling of both brain size and body mass will proceed this way separately. After both curves are fit a bivariate plot of the relationship between the curves (from the first derivatives) is developed, thus quantifying the allometric relationship between brain size and body mass over time.

Multivariate Adaptive Regression Splines

Multivariate Adaptive Regression Splines (MARS) can be used to model endocranial volume or body mass over time. This procedure is a non-parametric form of regression, generally used for high dimensional data (Friedman, 1991) because it automatically models non-linearities and interactions between variables. This is an extension of, and improvement on, the process of recursive partitioning. It uses a forward stepwise method to generate power spline functions; the resulting basis functions have continuity, unlike the step

functions produced in recursive partitioning (Team, 2013). The MARS model is built as

$$\hat{f}(x) = \sum_{i=1}^{k} c_i B_i(x) \tag{3.4}$$

where c_i is a constant and B_i represents "basis functions," in this case the intercept and a hinge function. At its core, MARS is simply a multivariate model that combines several univariate calculations and smoothing. The MARS algorithm includes a loop function that chooses the best placement for a "hinge" or "knot" based on marginal data values. One drawback of this procedure in this analysis is that it is sensitive to measurement errors and knot placement can be difficult in areas of locally high variance (Friedman, 1991). An advantage of MARS over regular linear or nonlinear regression is the series of fitted straight lines. The slopes of these lines as well as the position and number of "hinges" gives an indication of the rate and timing of changes in body size or brain size.

Chapter 4

Results

4.1 Body Mass Estimation

Body mass estimates (2.5%, point estimate, and 97.5%) for Profile Likelihood (PL), Classical Calibration (CC), and Inverse Calibration (IC) methods before removal of any individual measurements based on allometry values are given in Table 4.1. The effect of allometric departure on body mass estimation is well-illustrated by many of these specimens. For example, AL 333w-56 and AL 827-1, both of whom have highly significant R p-values (<0.001) do not have a 2.5% MLE estimator. AL 827-1 has five postcranial measurements and only two have exceedingly high allometry values. Removing those two offending measurements improves the estimate for this individual. The CC estimates collapse on a point for many individuals. Brown (1993, p: 89) describes this characteristic of R; "the more contradictory the observed $\bar{Z}$ the more restricted the confidence region." This is evident when the lower bound, point estimate, and upper bound are all the same (e.g., for Lucy (AL 288-1) each CC value is 18.2kg). Trinil I has CC values that are collapsed on a point at more than 380kg and an MLE range from nearly 264kg to 10,242kg, with a point estimate of 1,356kg.

These initial results illustrate the drastic effect that allometric and size differences can have in the estimation of body mass. This phenomenon has been documented previously in both stature and body mass (Konigsberg et al., 1998; Hens et al., 2000; Uhl et al., 2013). McHenry (1992a) highlights the differences in estimates with different reference samples and different regression techniques. This study uses the R and Rx statistics to mitigate some of the allometric and size effects in body mass estimation.

Some individuals with multiple available measurements had significant R p-values. In this case, (e.g., AL 827-1) measurements were removed based on high absolute allometric values or z-scores. The first round of measurement removal left only nine specimens that were still multivariate and had significant R p-values (see Table A1).

In many cases, high allometric departures were from femoral shaft measurements, particularly the Femoral Transverse Subtrochanteric diameter (FTST). A drawback of culling measurements from the literature is the enormous potential for interobserver error; even for something as basic as adequately defining a measurement.

Problems with Tibial Maximum Length are well-documented (see Jantz et al. (1994, 1995)), although that singular measurement is not a likely issue in this work. In the literature the femoral shaft measurements are sometimes referred to as proximal femoral measurements and sometimes, more specifically, as subtrochanteric measurements. Similarly, femoral epicondylar breadth is sometimes referred to as distal femoral breadth. The corresponding measurements of the reference sample follow the descriptions in Table 3.1.

A second round of removal of high absolute allometric scores left three specimens—AL 288-1 (Lucy), AL 827-1, and LB1. Lucy's body proportions have been subject to much debate (e.g., Jungers, 1982; Wolpoff, 1983; Jungers, 1988a). This analysis confirms that, compared to modern human body proportions Lucy can safely be classified as an extreme outlier. After removal of Humeral Maximum Length, Capitulum Height, Humeral Articular Width, Femoral Maximum Length, Femoral A-P Midshaft, Femoral Distal A-P Diameter, Femoral Distal Transverse Diameter, Tibial Maximum Length, Lucy had a non-significant R p-value.

Much debate surrounds *Homo floresiensis*, whose sole representative in this study is the LB1 specimen. One prevailing theory is that the species represents insular dwarves (scaled-down versions) of *Homo erectus* (Brown et al., 2004; Gordon et al., 2008). The initial values for LB1 are based on eight postcranial measurements. In the first iteration, FML was the most different allometrically, with a value of -5.928, not surprising given the very small size of LB1. After FML was removed FHD was the highest allometric value at 3.155. After a third iteration, HMSMin still exceeded the critical value at 2.658. Unfortunately, the body mass estimates for LB1 based on a modern human reference sample are unrealistic and thus, LB1 was removed from further analyses.

Table 3.3 shows the final body mass estimates. Bolded values were removed before further analyses.

Table 4.1: Body Mass Estimates Fossil Specimens and confidence intervals (kg) for all three estimators (Profile Likelihood (PL), Classical Calibration (CC), and Inverse Calibration (IC)), no critical values removed

Fossil Specimen	**PL 2.5%**	**PL**	**PL 97.5%**	**CC 2.5%**	**CC**	**CC 97.5%**	**IC 2.5%**	**IC**	**IC 97.5%**
KNM-KP 271	12.1	53.0	229.3	11.1	53.1	249.5	32.9	55.3	92.9
Stw 431	6.9	30.6	127.6	4.6	31.0	183.9	30.6	51.4	86.3
AL 128-1	0.1	1.8	10.6	0.7	2.4	4.1	23.5	40.2	68.6
AL 129-1b	NA	NA	NA	0.1	0.1	0.1	8.8	18.6	39.4

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Table 4.1 – continued from previous page

Fossil Specimen	**MLE 2.5%**	**MLE**	**MLE 97.5%**	**CC 2.5%**	**CC**	**CC 97.5%**	**IC 2.5%**	**IC**	**IC 97.5%**
AL 137-50	3.7	15.1	55.1	2.7	15.2	72.5	27.2	45.4	75.9
MAK-VP-1/1	0.6	4.8	26.2	1.0	5.5	18.2	25.7	43.8	74.6
AL 137-48a	0.8	4.9	22.3	6.4	6.4	6.4	24.5	41.5	70.3
AL 152-2	0.4	2.0	7.9	0.4	2.3	7.0	19.8	33.4	56.3
AL 211-1	0.4	2.1	8.2	0.5	2.4	6.8	20.0	33.7	56.7
AL 288-1	NA	NA	NA	18.1	18.1	18.1	17.7	44.1	109.3
AL 322-1	0.1	0.7	3.3	1.3	1.3	1.3	18.3	31.1	53.1
AL 333-131	18.2	107.6	698.9	99.7	99.7	99.7	34.7	59.1	100.5
AL 333-140	NA	NA	NA	0.2	0.2	0.2	10.4	21.4	43.7
AL 333-142	0.2	1.8	10.2	0.1	2.0	11.4	23.1	39.5	66.4
AL 333-3	3.1	13.7	53.3	16.1	16.1	16.1	21.1	45.5	76.3
AL 333-4	3.9	15.6	56.4	3.0	16.1	70.5	27.3	45.6	76.1
AL 333-95	6.8	38.7	210.6	6.2	39.1	229.8	31.6	53.7	91.0
AL 333w-40	9.8	56.8	328.7	17.3	56.7	186.3	32.8	55.8	94.7
AL 333w-56	NA	NA	NA	0.1	0.1	0.1	10.4	21.6	44.6
AL 827-1	NA	NA	NA	0.2	0.2	0.2	11.3	22.9	46.5
Sts 14	NA	0.17	2.1	4.1	4.1	4.1	23.0	39.9	69.4
Kromdraai	6.5	29.4	124.6	6.4	29.9	125.9	30.4	51.2	86.1
KNM-ER 1475	2.4	15.1	78.7	1.7	15.4	106.5	28.7	48.7	82.7
KNM-ER 1504	4.9	23.2	100.1	8.0	24.6	64.5	29.6	49.8	83.9
KNM-ER 1472	1.0	6.1	28.3	1.8	7.2	18.2	25.3	42.9	72.7
KNM-ER 1481	0.7	4.4	20.9	1.9	5.5	9.4	24.5	41.5	70.3
KNM-ER 1500d	0.0	0.6	3.2	0.9	0.9	0.9	19.3	33.1	56.6
KNM-ER 1503	0.3	2.3	11.3	3.2	3.2	3.2	22.8	38.8	66.0
KNM-ER 1809	0.07	0.6	3.4	1.1	1.1	1.1	19.7	33.7	57.8
KNM-ER 3728	0.1	1.4	7.2	2.2	2.2	2.2	21.6	36.9	62.9
KNM-ER 738	0.9	4.0	14.6	0.3	4.1	26.7	21.7	36.5	61.1

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Table 4.1 – continued from previous page

Fossil Specimen	MLE 2.5%	MLE	MLE 97.5%	CC 2.5%	CC	CC 97.5%	IC 2.5%	IC	IC 97.5%
KNM-ER 815	0.2	1.7	10.0	0.2	2.0	9.5	23.1	39.5	67.5
SK 24600	0.5	3.2	13.8	0.3	3.5	21.0	22.6	38.1	64.5
OH 62Y	0.1	0.9	4.8	1.4	1.4	1.4	20.4	35.0	59.7
TM 1517	1.9	9.3	38.5	11.2	11.2	11.2	26.0	43.9	73.9
Dmanisi 4167	4.0	16.6	63.0	5.3	17.4	48.6	27.8	46.5	77.9
KNM-ER 736	24.7	113.5	563.0	36.1	108.0	372.6	35.9	60.6	102.2
SK 82	0.6	3.2	13.3	4.9	4.9	4.9	22.2	37.5	63.3
SK 97	1.4	6.4	24.8	7.9	7.9	7.9	24.1	40.5	68.1
KNM-ER 3735A	0.6	4.4	21.9	7.3	7.3	7.3	24.8	42.2	71.7
KNM-ER 737	7.0	37.4	188.6	39.6	39.6	39.6	31.5	53.3	90.2
KNM-WT 15000	18.8	87.9	431.8	72.1	72.1	72.1	34.8	58.7	99.1
OH 20	1.4	9.5	50.5	1.4	10.1	50.7	27.4	46.7	79.3
KNM-ER 1463	0.07	0.7	3.9	1.4	1.4	1.4	20.4	34.9	59.8
KNM-ER 1465	5.6	31.9	167.4	3.4	31.9	260.6	31.0	52.5	89.1
KNM-ER 803	6.5	39.2	223.0	13.0	40.2	115.7	31.7	53.8	91.4
KNM-ER 993	76.3	693.5	11640.0	140.0	140.0	140.0	37.6	64.7	111.3
KNM-ER 739	32.9	154.1	806.9	132.0	132.0	132.0	37.0	62.6	105.8
KNM-ER 6020	36.3	170.9	913.3	142.8	142.8	142.8	37.4	63.3	106.9
SKX 10924	0.4	2.7	11.4	0.2	2.7	20.2	21.8	36.9	62.4
Trinil I	263.6	1355.8	10242.4	380.6	380.6	380.6	46.1	78.6	133.8
Broken Hill E691	58.7	217.1	894.2	43.1	216.5	1290.9	40.9	68.5	114.6
Ehringsdorf 5	32.3	89.9	256.0	87.5	87.5	87.5	38.0	62.1	101.3
Krapina 213	7.4	45.4	268.5	46.3	46.3	46.3	32.1	54.6	92.8
Krapina 214	0.7	5.3	28.8	0.9	5.9	24.3	25.9	44.1	75.2
Skhul III	38.7	106.9	304.3	46.1	105.5	253.1	39.6	64.7	105.5
Skhul IV	15.7	43.3	117.7	21.3	43.8	87.3	32.2	52.4	85.3
Skhul IX	16.4	96.6	613.7	91.0	91.0	91.0	34.4	58.5	99.6

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Table 4.1 – continued from previous page

Fossil Specimen	MLE 2.5%	MLE	MLE 97.5%	CC 2.5%	CC	CC 97.5%	IC 2.5%	IC	IC 97.5%
Skhul V	29.7	82.2	232.1	80.1	80.1	80.1	37.3	60.9	99.3
Skhul VI	18.4	50.5	137.2	21.6	50.7	117.5	33.4	54.4	88.4
Skhul VII	12.0	32.5	85.9	7.6	32.5	131.3	30.0	48.7	79.0
Tabun C1	12.2	35.5	100.6	37.8	37.8	37.8	30.8	50.3	82.3
Tabun C3	5.5	16.2	44.8	6.4	16.6	39.4	25.6	41.9	68.4
Tabun E1	14.5	39.9	107.9	10.4	40.0	149.1	31.6	51.4	83.5
Sedia-del-Diavolo	23.7	65.3	180.8	19.0	65.3	226.3	35.5	57.8	94.1
Bisceglie I	21.2	58.5	161.3	16.3	58.5	209.9	34.6	56.3	91.6
Kebarah M1	7.9	22.6	61.6	6.0	22.6	79.0	27.6	45.0	73.4
Kebarah M4	4.7	13.8	37.9	4.2	14.0	41.6	24.6	40.2	65.7
Kebarah M7	7.1	20.3	55.3	5.4	20.3	70.8	26.9	43.9	71.6
Kebarah P10	0.3	2.5	13.9	0.2	2.7	17.3	23.9	40.7	69.5
Kebarah P11	0.8	6.1	32.6	0.9	6.6	29.6	26.2	44.7	76.0
Kebarah P12	0.6	5.4	31.8	7.2	7.2	7.2	26.4	45.1	76.9
Kebarah P13	0.03	1.0	6.1	1.4	1.4	1.4	22.3	38.2	65.5
Kebarah P14	3.2	20.0	108.6	4.2	21.1	85.7	29.7	50.3	85.5
Kebarah P16	0.5	4.0	21.2	0.3	4.1	26.6	25.0	42.6	72.5
Kebarah P17	0.1	1.8	10.4	0.4	2.2	6.0	23.4	40.0	68.3
Kebarah P2	1.3	8.9	46.8	1.0	9.3	55.0	27.2	46.2	78.6
Kebarah P20	2.1	13.8	74.4	2.9	14.8	57.0	28.6	48.5	82.5
Kebarah P22	0.7	5.8	32.1	1.6	6.7	18.5	26.3	44.8	76.2
Kebarah P24	18.8	99.6	566.0	13.3	99.1	828.0	34.8	59.1	100.1
Kebarah P3	0.3	2.8	15.6	0.3	3.1	16.8	24.2	41.3	70.5
Kebarah P5	2.5	17.3	98.8	19.5	19.5	19.5	29.2	49.9	84.9
Kebarah P6	0.2	1.9	10.8	0.2	2.2	9.3	23.4	39.9	68.2
Kebarah P7	0.4	3.7	19.6	0.3	3.8	26.4	24.7	42.2	71.8
Kebarah P8	0.3	2.5	13.8	0.2	2.7	15.7	23.9	40.8	69.5

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Table 4.1 – continued from previous page

Fossil Specimen	**MLE 2.5%**	**MLE**	**MLE 97.5%**	**CC 2.5%**	**CC**	**CC 97.5%**	**IC 2.5%**	**IC**	**IC 97.5%**
Kebarah P9	1.5	9.7	50.1	0.9	9.8	71.7	27.4	46.5	79.0
Neanderthal I	20.7	54.6	143.4	9.7	54.6	304.4	34.2	55.4	89.7
Amud I	45.0	119.7	329.4	33.9	117.4	446.6	41.3	67.1	108.9
La Chapelle	21.8	57.8	153.8	13.2	57.8	254.5	34.7	56.2	91.1
La Quina 5	21.8	60.7	170.0	36.1	60.5	102.4	34.8	56.8	92.6
La Quina unn (B2)	6.8	40.6	230.7	12.9	41.5	124.7	31.8	54.0	91.7
Palomas 96	1.8	9.6	41.9	1.5	9.9	47.5	26.5	44.7	75.4
Shanidar IV	4.0	19.6	86.0	2.6	20.1	125.5	29.0	48.9	82.4
Hortus 34	2.4	15.1	79.6	2.0	15.6	90.1	28.7	48.8	82.8
St. Germaine la Rive	8.2	23.0	62.0	8.7	23.9	59.0	27.7	45.0	73.3
Veryier	9.3	25.8	69.0	7.8	26.4	81.3	28.4	46.2	75.1
La Ferrassie 1	16.9	79.3	387.1	31.5	77.1	202.5	34.4	58.0	97.5
La Ferrassie 2	5.2	25.9	117.1	5.8	27.0	107.6	30.1	50.7	85.6
Spy 2	20.3	54.9	148.4	18.2	54.9	165.1	34.1	55.5	90.1
Barma Grande I	48.1	250.5	1584.2	184.8	184.8	184.8	38.2	64.8	110.1
Barma Grande II	1.12	13.4	105.0	25.9	26.9	25.9	29.5	50.5	86.5
CroMagnon 1	45.2	126.2	366.4	119.7	119.7	119.7	41.0	67.0	109.4
Grotte des Enfants I	17.6	103.227	660.5	96.5	96.5	96.5	34.6	58.9	100.2
Grotte des Enfants III	0.5	4.4	24.3	0.8	5.0	19.1	25.5	43.4	74.0
Grotte des Enfants IV	72.8	324.2	1735.4	69.5	298.6	1838.1	40.8	68.9	116.4
La Rochette 1	13.2	36.5	98.9	9.2	36.7	139.0	30.9	50.3	81.9
Mladeč 1	1.9	14.0	80.9	16.4	16.4	16.4	28.8	49.1	83.5
Mladeč 6	18.4	52.4	149.2	52.6	52.6	52.6	33.6	54.9	89.7

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Table 4.1 – continued from previous page

Fossil Specimen	**MLE 2.5%**	**MLE**	**MLE 97.5%**	**CC 2.5%**	**CC**	**CC 97.5%**	**IC 2.5%**	**IC**	**IC 97.5%**
Paglicci I	30.8	85.8	243.7	82.7	82.7	82.7	37.7	61.4	100.2
Paviland I	21.0	57.1	154.9	21.0	57.0	154.8	34.4	56.0	91.0
Predmost III	28.4	81.4	237.4	77.7	77.7	77.7	37.0	60.5	99.01
Predmost IV	15.1	42.1	115.8	42.9	42.9	42.9	32.0	52.1	84.9
Predmost IX	9.9	27.7	75.4	17.3	28.8	44.0	29.0	47.2	76.9
Predmost X	11.0	32.0	90.5	34.0	34.0	34.0	30.1	49.2	80.4
Predmost XIV	12.0	34.0	93.9	35.3	35.3	35.3	30.5	49.7	80.9
San Teodoro 4	19.7	54.3	149.4	42.0	54.4	70.3	34.0	55.3	90.1
Willendorf 1	8.3	23.5	64.1	6.4	23.5	80.5	27.9	45.5	74.1
Brno 2	28.0	78.4	222.7	76.8	76.8	76.8	36.91	60.21	98.2
Cap Blanc I	5.7	16.3	43.4	4.4	16.8	54.8	25.4	41.3	67.2
Pataud 10	16.1	44.8	123.0	12.9	44.8	152.9	32.5	52.9	86.1
Font d foret I	24.2	65.8	179.9	34.7	65.4	125.1	35.6	57.9	94.2
La Madelaine	15.2	41.0	109.2	11.1	41.1	147.6	31.8	51.6	83.8
LB1	0.7	2.9	8.2	4.6	4.6	4.6	18.0	29.9	49.6
Chancellade	14.3	39.9	109.9	40.8	40.8	40.8	31.6	51.5	83.9
Le Peyrat 5	19.7	54.2	148.9	40.5	54.2	72.4	34.0	55.3	90.0
Le Peyrat 6	6.8	18.9	49.8	3.6	19.1	87.1	26.2	42.6	69.2
Obercassel I	10.2	28.2	75.7	9.6	28.9	80.2	29.1	47.3	76.8
Obercassel II	8.0	47.1	269.7	49.1	49.1	49.1	32.3	54.8	93.3
Sandalja 1	2.1	13.4	71.4	2.1	14.1	69.9	28.4	48.3	82.0
San Teodoro 1	29.2	79.4	219.1	39.1	78.0	162.3	37.2	60.5	98.5
Belt Cave 1	0.5	4.2	22.1	0.3	4.2	32.0	25.1	42.7	72.6
Belt Cave 3	1.8	12.7	71.7	14.6	14.6	14.6	28.5	48.5	82.5
Hotu 2	14.5	39.2	103.9	8.7	39.1	169.8	31.5	51.0	82.8
Hotu 3	6.7	19.1	51.5	4.6	19.4	72.4	26.5	43.1	70.2
Combe-Capelle 1	4.4	20.9	90.3	2.1	21.0	166.3	29.2	49.2	82.8

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Table 4.1 – continued from previous page

Fossil Specimen	**MLE 2.5%**	**MLE**	**MLE 97.5%**	**CC 2.5%**	**CC**	**CC 97.5%**	**IC 2.5%**	**IC**	**IC 97.5%**
Culoz 1	12.7	34.8	93.5	11.6	35.4	102.0	30.6	49.7	80.8
Culoz 2	9.8	27.4	73.6	10.5	28.2	69.4	28.9	46.9	76.4
Montardit 3	5.5	15.4	40.9	3.3	15.8	63.3	25.0	40.6	66.0

Table 4.2 shows the R and Rx p-values for each fossil specimen that has at least two postcranial measurements available in the literature. Statistically significant (at $\alpha = 0.05$) values are in bold. Statistical significance indicates that the specimen departs in allometry (R) or size (Rx) from the modern human reference sample.

Table 4.2: R and Rx p-values for Fossil Specimens

Fossil Specimen	**Date (mya)**	***R* p-value**	***Rx* p-value**
KNM-KP 271	4.1	0.166	0.950
Stw 431	4.0	0.381	0.447
AL 128-1	3.4	**0.011**	< **0.001**
AL 129-1b	3.4	< **0.001**	< **0.001**
AL 137-50	3.4	0.514	0.071
MAK-VP-1/1	3.4	**0.041**	**0.008**
AL 137-48a	3.1	**0.004**	**0.005**
AL 152-2	3.1	0.055	< **0.001**
AL 211-1	3.1	**0.046**	< **0.001**
AL 288-1	3.1	< **0.001**	< **0.001**
AL 322-1	3.1	< **0.001**	< **0.001**
AL 333-131	3.1	**0.005**	0.508
AL 333-140	3.1	< **0.001**	< **0.001**

Continued on next page

Table 4.2 – continued from previous page

Fossil Specimen	Date (mya)	R p-value	Rx p-value
AL 333-142	3.1	0.153	< **0.001**
AL 333-3	3.1	**0.004**	0.079
AL 333-4	3.1	0.262	0.079
AL 333w-40	3.1	**0.040**	0.982
AL 333w-56	3.1	< **0.001**	< **0.001**
AL 827-1	3.1	< **0.001**	< **0.001**
Sts 14	2.6	< **0.001**	**0.001**
Kromdraai	2.5	0.142	0.422
KNM-ER 1475	2.0	0.396	0.144
MH1	1.96	<**0.001**	<**0.001**
MH2	1.96	**0.002**	<**0.001**
KNM-ER 1504	1.9	**0.048**	0.289
KNM-ER 1472	1.9	**0.037**	**0.010**
KNM-ER 1481	1.9	**0.019**	**0.003**
KNM-ER 1500d	1.9	**0.004**	< **0.001**
KNM-ER 1503	1.9	**0.004**	< **0.001**
KNM-ER 1809	1.9	**0.001**	< **0.001**
KNM-ER 3728	1.9	**0.001**	< **0.001**
KNM-ER 738	1.9	0.730	< **0.001**
KNM-ER 815	1.9	0.081	< **0.001**
SK 24600	1.0	0.309	< **0.001**
OH 62Y	1.8	**0.002**	< **0.001**
TM 1517	1.75	**0.129**	**0.0299**
Dmanisi 4167	1.7	0.056	0.107
KNM-ER 736	1.7	0.057	0.404
SK 82	1.7	< **0.001**	< **0.001**
SK 97	1.7	**0.010**	**0.005**
KNM-ER 3735A	1.6	< **0.001**	**0.008**

Continued on next page

Table 4.2 – continued from previous page

Fossil Specimen	**Date (mya)**	***R* *p*-value**	***Rx* *p*-value**
KNM-ER 737	1.6	**0.002**	0.670
KNM-WT 15000	1.6	< **0.001**	0.680
OH 20	1.6	0.128	0.053
KNM-ER 1463	1.5	< **0.001**	< **0.001**
KNM-ER 1465	1.5	0.860	0.529
KNM-ER 803	1.5	**0.034**	0.712
KNM-ER 993	1.5	< **0.001**	0.190
KNM-ER 739	1.4	**0.001**	0.262
KNM-ER 6020	1.4	**0.001**	0.221
SKX 10924	1.0	0.872	< **0.001**
Trinil I	1.0	< **0.001**	**0.004**
Broken Hill E691	0.3	0.654	0.061
Ehringsdorf 5	0.15	**0.020**	0.433
Krapina 213	0.1	**0.012**	0.835
Krapina 214	0.1	0.071	**0.011**
Skhul III	0.1	0.65	0.274
Skhul IV	0.1	0.055	0.675
Skhul IX	0.1	**0.008**	0.577
Skhul V	0.1	**0.006**	0.525
Skhul VI	0.1	**0.078**	0.869
Skhul VII	0.1	0.965	0.347
Tabun C1	0.075	**0.001**	0.491
Tabun C3	0.075	0.073	**0.039**
Tabun E1	0.075	0.544	0.568
Sedia-del-Diavolo	0.07	0.531	0.785
Bisceglie I	0.064	0.866	0.932
Kebarah M1	0.06	0.785	0.124
Kebarah M4	0.06	0.217	**0.018**

Continued on next page

Table 4.2 – continued from previous page

Fossil Specimen	**Date (mya)**	***R* *p*-value**	***Rx* *p*-value**
Kebarah M7	0.06	0.763	0.085
Kebarah P10	0.06	0.250	**0.001**
Kebarah P11	0.06	0.089	**0.016**
Kebarah P12	0.06	**0.003**	**0.021**
Kebarah P13	0.06	**0.005**	<**0.001**
Kebarah P14	0.06	0.072	0.271
Kebarah P16	0.06	0.279	**0.003**
Kebarah P17	0.06	**0.021**	<**0.001**
Kebarah P2	0.06	0.220	**0.042**
Kebarah P20	0.06	0.064	0.134
Kebarah P22	0.06	**0.029**	**0.017**
Kebarah P24	0.06	0.460	0.513
Kebarah P3	0.06	0.139	**0.001**
Kebarah P5	0.06	**0.010**	0.234
Kebarah P6	0.06	0.060	<**0.001**
Kebarah P7	0.06	0.398	**0.002**
Kebarah P8	0.06	0.169	**0.001**
Kebarah P9	0.06	0.541	**0.049**
Neanderthal I	0.055	0.854	0.973
Amud I	0.054	0.300	0.190
La Chapelle	0.05	0.466	0.947
La Quina 5	0.05	**0.036**	0.886
La Quina unn (B2)	0.05	**0.036**	0.739
Palomas 96	0.05	0.207	**0.030**
Shanidar IV	0.044	0.382	0.201
Hortus 34	0.04	0.197	0.150
St. Germaine la Rive	0.04	0.099	0.138

Continued on next page

Table 4.2 – continued from previous page

Fossil Specimen	**Date (mya)**	***R* *p*-value**	***Rx* *p*-value**
Veryier	0.04	0.198	0.191
La Ferrassie 1	0.038	**0.039**	0.682
La Ferrassie 2	0.038	0.106	0.363
Spy 2	0.036	0.167	0.981
Barma Grande I	0.03	<**0.001**	0.131
Barma Grande II	0.03	<**0.001**	0.337
CroMagnon I	0.03	**0.009**	0.185
Grotte des Enfants I	0.03	**0.008**	0.533
Grotte des Enfants III	0.03	0.056	**0.007**
Grotte des Enfants IV	0.03	0.133	**0.035**
La Rochette 1	0.03	0.431	0.473
Mladeč 1	0.03	**0.006**	0.167
Mladeč 6	0.03	**0.004**	0.923
Paglicci I	0.03	**0.003**	0.487
Paviland I	0.03	0.120	0.966
Predmost III	0.03	<**0.001**	0.487
Predmost IV	0.03	**0.015**	0.647
Predmost IX	0.03	**0.034**	0.248
Predmost X	0.03	<**0.001**	0.386
Predmost XIV	0.03	**0.008**	0.424
San Teodoro 4	0.03	**0.028**	0.969
Willendorf 1	0.03	0.601	0.141
Brno 2	0.024	**0.016**	0.577
Cap Blanc I	0.021	0.245	**0.036**
Pataud 10	0.021	0.520	0.711

Continued on next page

Table 4.2 – continued from previous page

Fossil Specimen	**Date (mya)**	***R* *p*-value**	***Rx* *p*-value**
Font de foret 1	0.02	**0.043**	0.778
La Madelaine	0.02	0.501	0.597
LB1	0.018	**<0.001**	**<0.001**
Chancellade	0.017	**0.014**	0.587
Le Peyrat 5	0.017	**0.028**	0.964
Le Peyrat 6	0.017	0.783	0.061
Obercassel I	0.015	0.140	0.251
Obercassel II	0.15	**<0.001**	0.874
Sandalja I	0.0123	0.123	0.120
San Teodoro 1	0.01	0.055	0.553
Belt Cave 1	0.009	0.615	**0.004**
Belt Cave 3	0.009	**0.011**	0.130
Hotu 2	0.009	0.614	0.543
Hotu 3	0.009	0.434	0.068
Combe-Capelle 1	0.007	0.845	0.221
Culoz 1	0.007	0.156	0.427
Culoz 2	0.007	0.098	0.232
Montardit 3	0.007	0.522	**0.027**

Table 4.3 shows allometry values and z-scores for fossil specimens with significant R values. As expected, those specimens with highly significant R scores have high positive or negative allometric values and z-scores. Bold values in Table 4.3 were removed and R recalculated (see Table A1).

Table 4.3: Allometry Values and z-scores for Fossil Specimens with Significant R p-values, no critical values removed

Fossil Specimen	***R* *p*-value**	**Allometry values**	**z scores**
AL 128-1	0.011	FAPST (-0.896); **FTST (2.394)**	NA
AL 129-1b	<0.001	**FDAPD (-18.206)**; FDTD (7.795); FECB (13.755)	FDAPD (-22.267); FDTD (3.651); FECB (15.227)
MAK-VP-1/1	0.041	FAPST (-0.715); **FTST (1.911)**	NA
AL 137-48a	0.004	HECB (0.607); **CapH (-2.765)**; HAW (1.699)	HECB (1.608); CapH (-3.084); HAW (2.023)
AL 211-1	0.047	FHD (1.356); **FAPST (-2.049)**; FTST (0.315)	FHD (1.017); FAPST (-3.261); FTST (2.010)
AL 288-1	<0.001	HML (8.967); HHD (0.101); HECB (1.986); CapH (-2.202); HAW (2.434); RHD (1.127); FML (-6.715); FHD (2.954); FAPST (-1.486); FTST (3.754); FAPMS (-3.972); **FDAPD (-30.811)**; FDTD (2.496); FECB (9.780); TML (-7.169)	HML (7.212); HHD (-0.630); HECB (0.447); CapH (-2.507); HAW (0.961); RHD (0.189); FML (-1.600); FHD (-1.174); FAPST (-0.783); FTST (2.785); FAPMS (-2.800); FAPD (-25.618); FDTD (2.413); FECB (9.709); TML (-1.453)
AL 322-1	<0.001	HECB (0.988); CapH (1.689); HAW (2.384); **FHD (-3.269)**	HECB (1.190); CapH (1.624); HAW (1.222); FHD (-4.651)
AL 333-131	0.006	FAPST (-0.963); **FTST (2.575)**	NA
AL 333-140	<0.001	**FDAPD (-16.711)**; FDTD (7.111); FECB (12.662)	FDAPD (-20.510); FDTD (3.397); FECB (13.993
AL 333-3	0.004	FML (-2.105); FHD (-0.391); FAPST (1.232); **FTST (2.639)**	FML (-2.650); FHD (-2.254); FAPST (0.499); FTST (3.131)
AL 333w-40	0.040	FAPST (-0.718); **FTST (1.920)**	NA
AL 333w-56	<0.001	FDAPD (-15.115); **FDTD (16.545)**	NA

Continued on next page

Table 4.3 – continued from previous page

Fossil Specimen	*R p*-value	Allometry values	z scores
AL 827-1	<0.001	FHD (13.261); FAPST (1.744); FTST (3.916); FAPMS (1.316); **FDAPD (-16.484)**	FHD (4.461); FAPST (-0.654); FTST (5.080); FAPMS (1.756); FDAPD (-14.258)
Sts 14	<0.001	**FAPST (5.127)**; FTST (-1.818)	NA
KNM-ER 1504	0.048	**HECB (1.812)**; CapH (-1.665); HAW (-0.117)	HECB (2.434); CapH (-1.997); HAW (-0.064)
KNM-ER 1472	0.038	FML (0.101); FAPST (-0.919); **FTST (2.388)**	FML (-0.272); FAPST (-2.877); FTST (2.846)
KNM-ER 1481	0.019	FML (0.202); FAPST (-1.074); **FTST (2.593)**	FML (-0.173); FAPST (-3.266); FTST (3.105)
KNM-ER 1500d	0.004	**FML (-2.514)**; FAPST (1.509); FTST (1.559)	FML (-1.740); FAPST (-0.994); FTST (2.506)
KNM-ER 1503	0.005	FML (-1.925); FAPST (0.671); **FTST (2.577)**	FML (-2.059); FAPST (-1.512); FTST (3.269)
KNM-ER 1809	0.001	**FML (-2.803)**; FAPST (1.683); FTST (1.738)	FML (-2.158); FAPST (-0.742); FTST (2.666)
KNM-ER 3728	0.002	FML (0.628); FAPST (-1.599); **FTST (3.096)**	FML (0.334); FAPST (-4.546); FTST (3.790)
OH 62Y	0.002	**FML (-2.366)**; FAPST (2.315); FTST (-1.086)	FML (-0.549); FAPST (0.878); FTST (-0.283)
TM 1517	0.013	HML (-1.804); HECB (0.688); CapH (-1.427); **HAW (2.240)**	HML (-1.001); HECB (1.109); CapH (-1.699); HAW (2.124)
SK 82	<0.001	**FML (-3.214)**; FHD (-0.202); FAPST (1.888); FTST (2.028)	FML (-2.746); FHD (-2.426); FAPST (0.901); FTST (2.973)
SK 97	0.010	FML (-2.107); FHD (0.154); FAPST (0.489); **FTST (2.561)**	FML (-2.022); FHD (-1.818); FAPST (-0.582); FTST (3.285)

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Table 4.3 – continued from previous page

Fossil Specimen	*R p*-value	Allometry values	z scores
KNM-ER 3735A	<0.001	**HECB (3.711)**; CapH (-1.085); HAW (-2.071)	HECB (4.514); CapH (-1.404); HAW (-2.810)
KNM-ER 737	0.002	FML (0.445); FAPST (-1.463); **FTST (3.137)**	FML (-0.866); FAPST (-2.716); FTST (3.251)
KNM-WT 15000	<0.001	**HMSMax (5.275)**; HMSMin (-1.717); HECB (-2.449); CapH (-4.337); UML (1.113); FML (-1.703); FHD (1.637); FAPST (0.304); FTST (0.173); TML (0.473)	HMSMax (5.277); HMSMin (-0.801); HECB (-2.363); CapH (-4.559); UML (0.500); FML (-1.001); FHD (0.690); FAPST (0.753); FTST (0.537); TML (0.046)
KNM-ER 1463	<0.001	**FML (-3.249)**; FAPST (2.028); FTST (1.795)	FML (-2.711); FAPST (-0.194); FTST (2.685)
KNM-ER 803	0.034	FAPST (0.743); **FTST (1.988)**	NA
KNM-ER 993	<0.001	FML (-5.343); FAPST (-2.812); FTST (1.174); **FECB (5.854)**	FML (-5.566); FAPST (-3.099); FTST (0.413); FECB (6.613)
KNM-ER 739	0.001	HECB (1.720); CapH (1.758); **HAW (-2.741)**	HECB (1.300); CapH (1.830); HAW (-3.423)
KNM-ER 6020	0.001	HECB (2.922); CapH(0.138); HAW (-2.412)	**HECB (2.935)**; CapH (-0.124); HAW (-2.750)
Trinil I	<0.001	FML (-1.539); FHD (-4.243); **FECB (5.888)**	FML (-4.708); FHD (-5.492); FECB (7.560)
Ehringsdorf 5	0.020	FAPST (-1.930); **FTST (2.457)**; FAPMS (0.200); FTMS (0.209)	FAPST (-2.371); FTST (2.033); FAPMS (-0.027); FTMS (-0.060)
Krapina 213	0.012	FAPST (-0.880); **FTST (2.351)**	NA
Skhul IX	0.008	FAPST (-0.926); **FTST (2.476)**	NA

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Table 4.3 – continued from previous page

Fossil Specimen	***R p*-value**	**Allometry values**	**z scores**
Skhul V	0.006	HML (2.079); FML (0.278); **FAPMS (2.374)**; FTMS (-1.602)	HML (0.882); FML (-0.077); FAPMS (2.334); FTMS (-2.239)
Tabun C1	0.001	HML (-0.667); RML (-0.083); UML (0.825); FML (1.016); FAPST (-1.971); FTST (1.983); FAPMS (-1.390); FTMS (0.668); **TML (-3.842)**	HML (0.075); RML (0.295); UML (0.827); FML (0.425); FAPST (-1.499); FTST (1.827); FAPMS (-1.166); FTMS (0.672); TML (-2.134)
Kebarah P12	0.003	FAPST (-1.028); **FTST (2.747)**	NA
Kebarah P13	0.005	FAPST (-0.982); **FTST (2.624)**	NA
Kebarah P17	0.021	FAPST (-0.808); **FTST (2.161)**	NA
Kebarah P22	0.029	FAPST (-0.763); **FTST (2.040)**	NA
Kebarah P5	0.010	FAPST (-0.902); **FTST (2.410)**	NA
La Quina 5	0.036	FAPST (-1.216); **FTST (2.021)**; FAPMS (-1.629); FTMS (0.579)	FAPST (-1.273); FTST (1.854); FAPMS (-1.702); FTMS (0.552)
La Quina unn (B2)	0.036	FAPST (-0.733); **FTST (1.961)**	NA
La Ferrassie 1	0.039	FML (-0.617); FAPST (-0.352); **FTST (2.444)**	FML (-1.821); FAPST (-0.823); FTST (2.445)
Barma Grande I	<0.001	FML (1.367); FAPST (-2.238); **FTST (3.197)**	FML (-0.528); FAPST (-2.747); FTST (2.966)
Barma Grande II	<0.001	FML (2.445); FAPST (-3.561); **FTST (4.458)**	FML (-0.528); FAPST (-5.772); FTST (4.615)
CroMagnon 1	0.009	FAPST (-1.136); FTST (1.651); **FAPMS (2.640)**; FTMS (-0.715)	FAPST (-1.842); FTST (1.084); FAPMS (2.250); FTMS (-1.234)
Grotte des Enfants I	0.008	FAPST (-0.930); **FTST (2.485)**	NA
Mladeč 1	0.006	FAPST (-0.969); **FTST (2.591)**	NA

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Table 4.3 – continued from previous page

Fossil Specimen	*R p*-value	Allometry values	z scores
Mladeč 6	0.004	**FAPMS (2.672)**; FTMS (-1.120)	NA
Paglicci I	0.003	FML (-1.323); FAPST (-1.551); FTST (2.057); **FAPMS (2.741)**; FTMS (-0.065)	FML (-2.263); FAPST (-1.967); FTST (1.852); FAPMS (2.658); FTMS (-0.677)
Predmost III	<0.001	FML (1.147); **FAPST (-3.386)**; FTST (3.129); FAPMS (0.016); FTMS (0.234)	FML (0340); FAPST (-3.689); FTST (2.789); FAPMS (0.127); FTMS (-0.106)
Premost IV	0.015	FML (-1.268); FAPST (-1.674); **FTST (2.765)**; FAPMS (0.053); FTMS (0.552)	FML (-1.384); FAPST (-1.909); FTST (2.785); FAPMS (0.113); FTMS (-0.213)
Predmost IX	0.034	FML (0.890); FAPST (-2.102); **FTST (2.240)**; FAPMS (-0.445); FTMS (0.140)	FML (1.002); FAPST (-2.387); FTST (2.422); FAPMS (-0.134); FTMS (-0.848)
Predmost X	<0.001	FML (-1.002); FAPST (-2.455); **FTST (3.274)**; FAPMS (-1.234); FTMS (1.003)	FML (-0.738); FAPST (-2.633); FTST (3.331); FAPMS (-1.081); FTMS (0.257)
Predmost XIV	0.008	FML (0.926); **FAPST (-2.598)**; FTST (2.324); FAPMS (-0.827); FTMS (0.408)	FML (1.032); FAPST (-2.829); FTST (2.380); FAPMS (-0.552); FTMS (-0.272)
San Teodoro 4	0.028	FML (-1.419); FAPST (-1.059); **FTST (2.764)**; FAPMS (0.073); FTMS (0.363)	FML (-1.819); FAPST (-1.236); FTST (2.695); FAPMS (0.027); FTMS (-0.258)
Brno 2	0.016	FAPST (-1.465); FTST (1.636); **FAPMS (2.298)**; FTMS (-0.466)	FAPST (-2.111); FTST (1.346); FAPMS (2.133); FTMS (-1.186)
Font de foret I	0.043	**FML (-1.909)**; FAPMS (1.603); FTMS (0.248)	FML (-2.110); FAPMS (1.435); FTMS (0.181)

Continued on next page

Table 4.3 – continued from previous page

Fossil Specimen	*R p*-value	Allometry values	z scores
LB1	<0.001	HMSMax (0.751); HMSMin(3.300); **FML (-5.928)**; FHD (-1.444); FAPST (-0.637); FTST (0.265); FAPMS (-0.512); FTMS (1.497)	HMSMax (1.020); HMSMin (3.054); FML (-3.487); FHD (-2.068); FAPST (-0.949); FTST (1.221); FAPMS (-0.022); FTMS (-0.142)
Chancellade	0.014	FML (-1.801); FAPST (-1.589); **FTST (2.426)**; FAPSM (0.662); FTMS (0.626)	FML (-1.802); FAPST (-1.863); FTST (2.493); FAPMS (0.714); FTMS (-0.185)
Le Peyrat 5	0.028	FML (-1.749); FAPST (1.132); FTST (-0.109); **FAPMS (2.510)**; FTMS (-0.440)	FML (-2.088); FAPST (0.923); FTST (0.018); FAPMS (2.403); FTMS (-1.014)
Obercassel II	<0.001	FML (-1.673); FAPST (-0.073); **FTST (4.111)**	FML (-3.448); FAPST (-1.198); FTST (4.272)
Belt Cave 3	0.011	FAPST (-0.892); **FTST (2.384)**	NA

4.2 Brain/Body Mass Relationships

4.2.1 Spearman's Rank Order Correlation

Spearman's rank order correlation was used to generally assess the trends of both brain size and body size over time. This is a non-parametric procedure that evaluates the correlation of a continuous variable with a ranked variable. In this case, "Date" is ordinal and either "Endocranial Volume" or "Body Mass Estimate" is the continuous variable. Because dates get smaller as they get more recent the Spearman correlations are all negative.

Table 4.4: Spearman's Rank Correlation Coefficients

Variables	**Spearman's Rho**	***p*-value**
Endocranial Volume/Date	-0.878	<0.001
Endocranial Volume/Date (2 mya—present)	-0.786	<0.001
Endocranial Volume/Date (Purported ancestors plus Neanderthals)	-0.825	<0.001
Body Mass/Date	-0.218	0.020
Body Mass/Date (2 mya—present)	0.005	0.969
Body Mass/Date (Purported ancestors plus Neanderthals)	-0.110	0.290

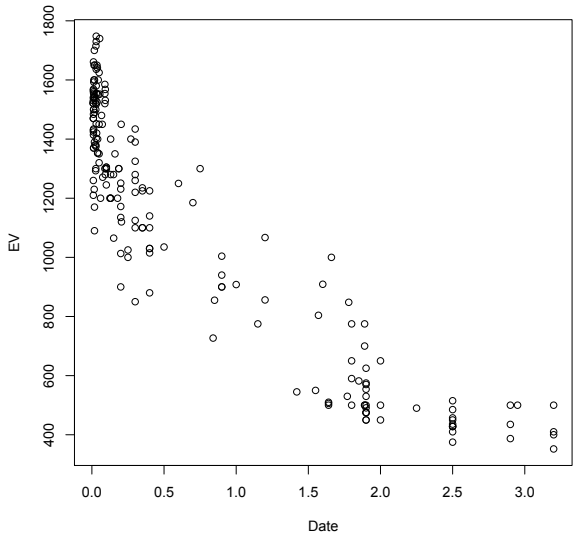

Figure 4.1: Endocranial Volume (CC) plotted against Date (Entire Sample)

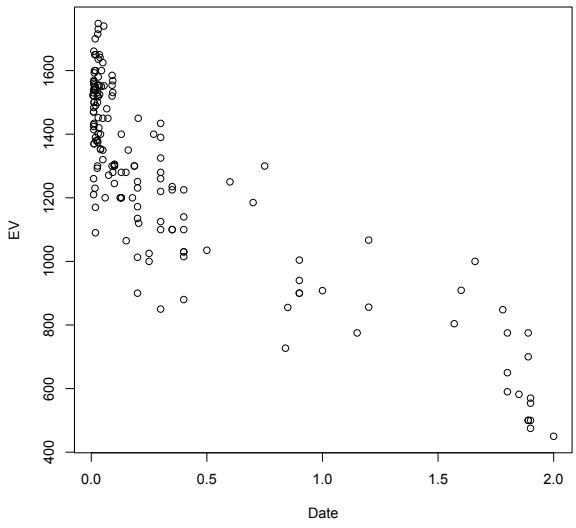

Figure 4.2: Endocranial Volume (CC) plotted against Date (2 mya—present)

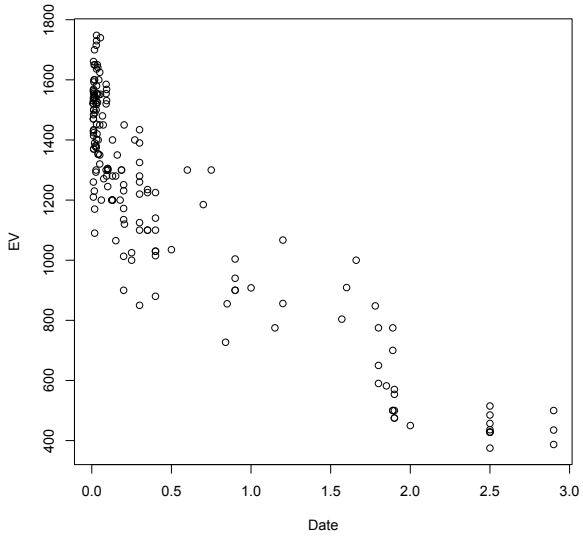

Figure 4.3: Endocranial Volume (CC) plotted against Date (Purported Ancestors—all *Homo*)

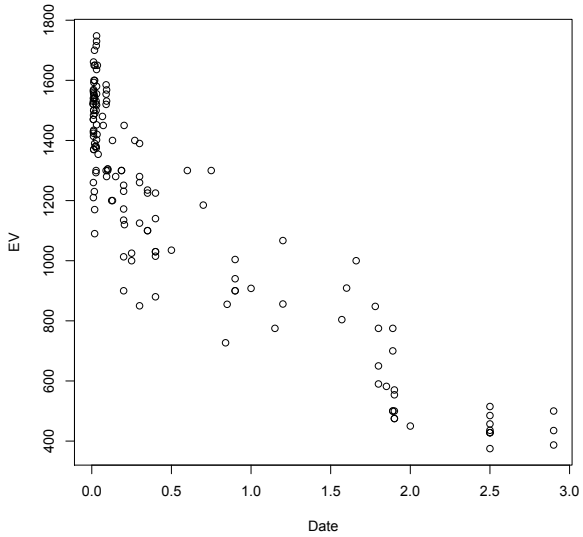

Figure 4.4: Endocranial Volume (CC) plotted against Date (Purported Ancestors—*Homo*)

The plots and correlation coefficients are not unexpected, but they only tell us very generally that brain size has increased over time. That increase has clearly not been linear, as is shown in both Figures 4.1 and 4.2. Figure 4.2 differs from Figure 4.1 because the time span has been shortened from more than 3 mya to 2 mya and non-*Homo* specimens from less than 2 mya have been removed (see Table 3.7). Figure 4.2 does

include individuals that are not directly ancestral to *Homo sapiens* (e.g., Neanderthals). Figure 4.3 shows the purported *Homo sapiens* ancestors (i.e., *Australopithecus africanus, Homo habilis, Homo erectus sensu lato, Homo sapiens*)(see Table 3.8), as with Figure 4.2 Neanderthals are included; Figure 4.4 shows the same purported ancestral lineage with Neanderthals removed. There is little discernible difference between analyses of data shown in Figures 4.3 and 4.4.

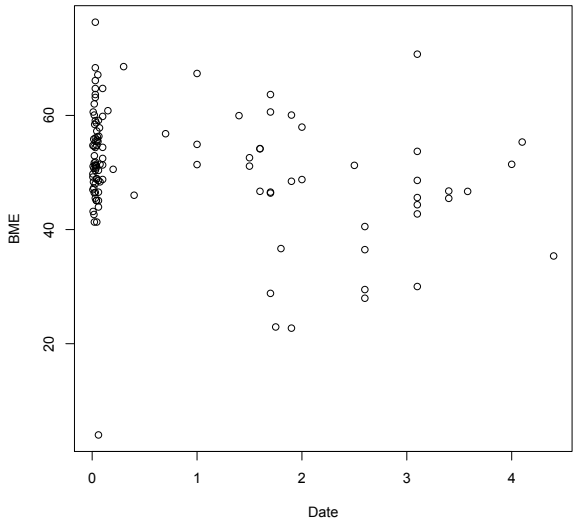

Figure 4.5: Body Mass Estimates (kg) plotted against Date (Entire Sample)

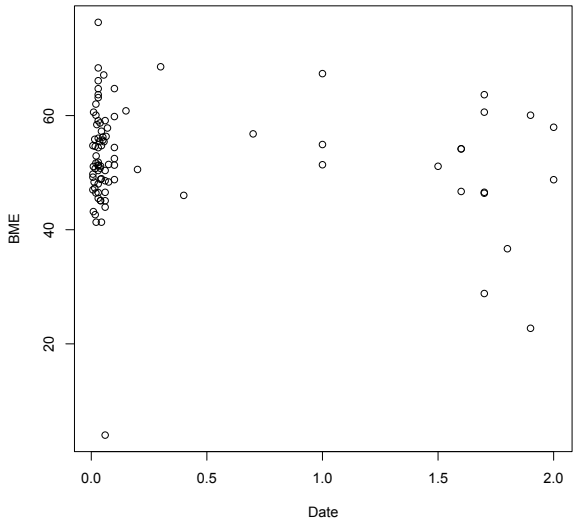

Figure 4.6: Body Mass Estimates (kg) plotted against Date (2 mya—present)

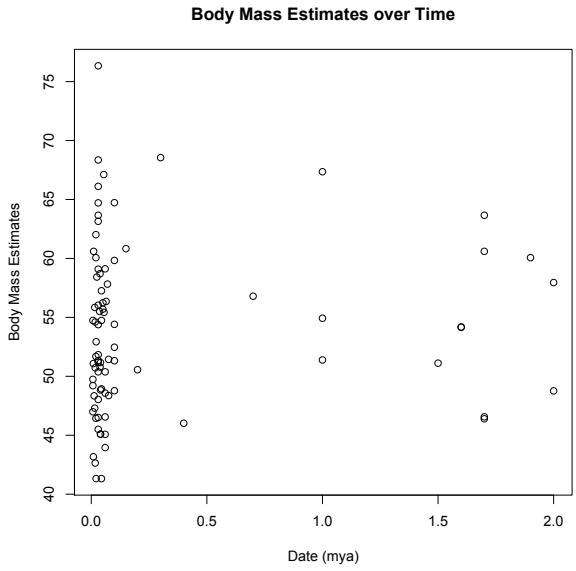

Figure 4.7: Body Mass Estimates (kg) plotted against Date (2mya—present), Outliers removed

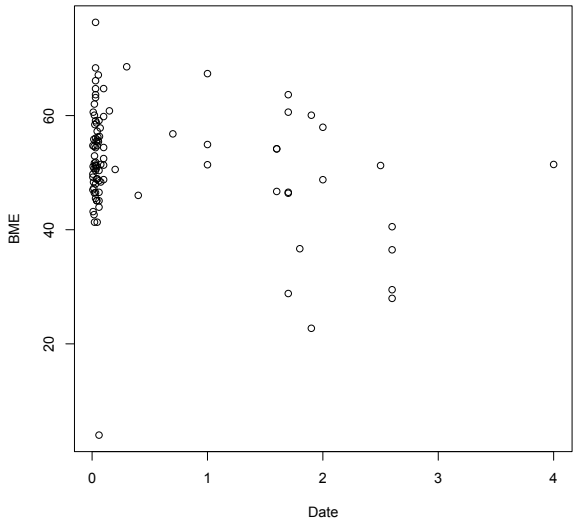

Figure 4.8: Body Mass Estimates (kg) plotted against Date (Purported Ancestors and *Homo*)

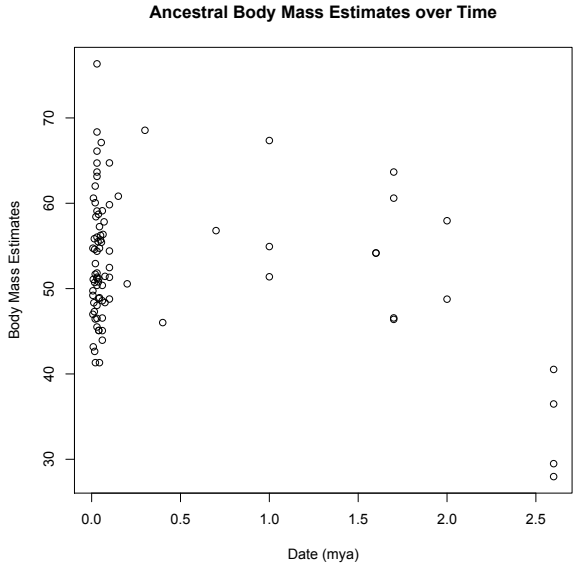

Figure 4.9: Body Mass Estimates (kg) plotted against Date Purported Ancestors and *Homo*), Outliers removed)

Body mass has a much weaker association with time. Data for Figure 4.5 comes from Table 3.3. There are sampling issues with the body mass data; not only are there fewer specimens available from earlier hominins, those that are available are generally more fragmentary and yield body mass estimates that cannot be used.

Data sets for Figures 4.6 and 4.8 are found in Tables 3.4 and 3.5. These data sets are similar to those for EV. Analyses include the entire sample, then a *Homo*-only set from 2.0 mya and later, and finally a purported ancestral lineage. Because of the similarity of EV analyses with and without Neanderthals, Neanderthals are included in all body mass analyses of *Homo*.

4.2.2 Hubert Test

The Hubert test is a non-parametric test that can incorporate a continuous variable over time described as a discrete variable (Konigsberg, 1990). Several studies of temporal trends in brain size or other cranial variables have employed it (Leigh, 1992a; Wood et al., 1994; Elton et al., 2001; Hawks, 2011). The Hubert test converts time estimates on a continuous scale into an ordinal rank variable. The Γ index value is between -1 and 1 and indicates the concordance of two vectors of data. In this case one vector is the data (either EV or body mass estimates) ranked by time and the second vector is the same data but it is permuted. The index indicates how much agreement there is between pairs of observed and permuted data.

Table 4.5 shows the results of the Hubert test for four data sets. Data sets (Entire Sample, 2 mya-present, Purported Ancestry plus Neanderthals, Purported Ancestry with Neanderthals removed) are as described in the previous section.

Table 4.5: Hubert Gamma coefficients and p-values for Endocranial Volume/Date

Data Set	Γ **index**	p**-value**
Endocranial Volume/Date (Entire Sample)	-0.92	0.001
Endocranial Volume/Date (2 mya—present)	-0.84	0.001
Endocranial Volume/Date (Purported ancestors, plus Neanderthals)	-0.90	0.001
Body Mass Estimates/Date (Entire Sample)	-0.35	0.001
Body Mass Estimates/Date (2 mya—present)	-0.19	0.041
Body Mass Estimates/Date (Purported ancestors, plus Neanderthals)	-0.35	0.001

The interpretation of the Hubert Test Γ is similar to a correlation coefficient. The Γ index is a concordance of permuted data with the observed data. For endocranial volume data, concordance is -0.92. This indicates a strong trend toward larger brain size as most of the permuted (expected) data does not agree with the observed data. Body mass over time has lower concordance values. The trend of increasing body mass is not as strong as increasing brain size. In this case, the three Γ values are not as similar as the brain size. The Γ value for the past 2 mya is higher (more negative) than the other two samples.

4.2.3 Fractional Polynomials

Fractional polynomials were fit to EV over time as well as body mass over time. Figure 4.10 shows a nonlinear association between Endocranial Volume and Date. This curve is fit as $EV = 1581 - 712 * \sqrt{date}$. The first derivative is $-\frac{356}{\sqrt{date}}$.

Figure 4.13 illustrates the relationship between body mass and date. This polynomial was fit as a simple linear model. There is no derivative, but the constant (slope) is -2.462.

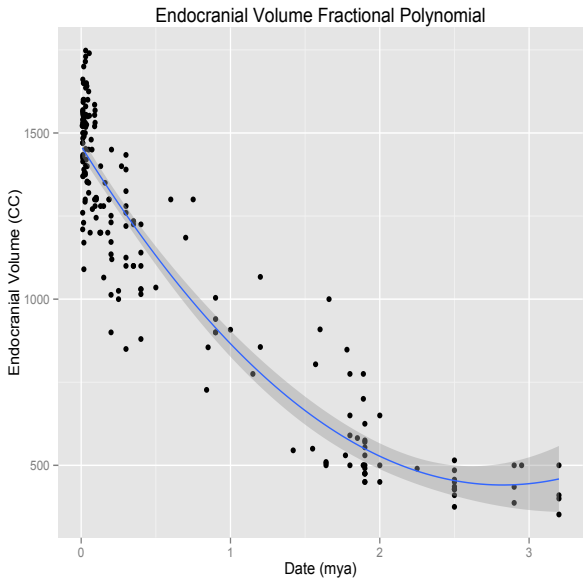

Figure 4.10: Polynomial Fit for Endocranial Volume (CC) over Time

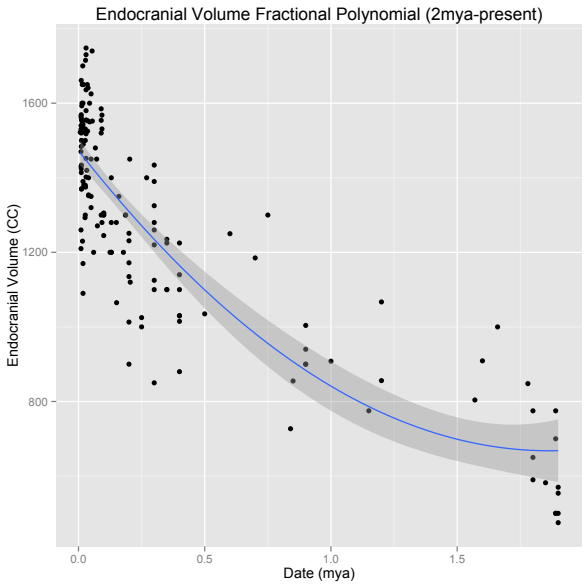

Figure 4.11: Polynomial Fit for Endocranial Volume (CC) over Time (2mya - present)

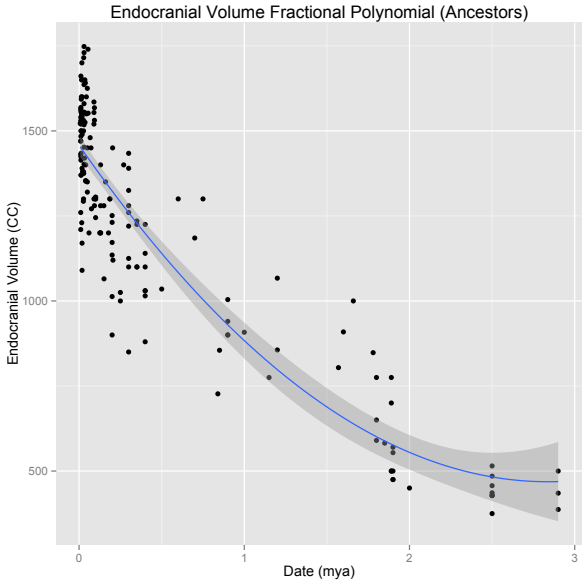

Figure 4.12: Polynomial Fit for Endocranial Volume (CC) over Time (Ancestors)

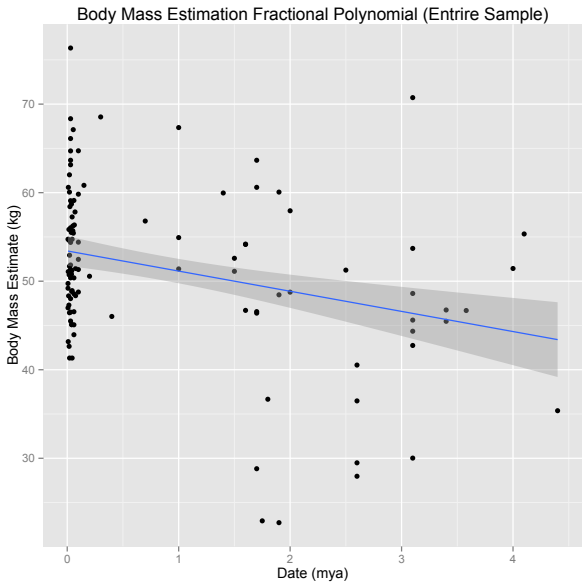

Figure 4.13: Polynomial Fit for Body Mass Estimates (kg) over Time

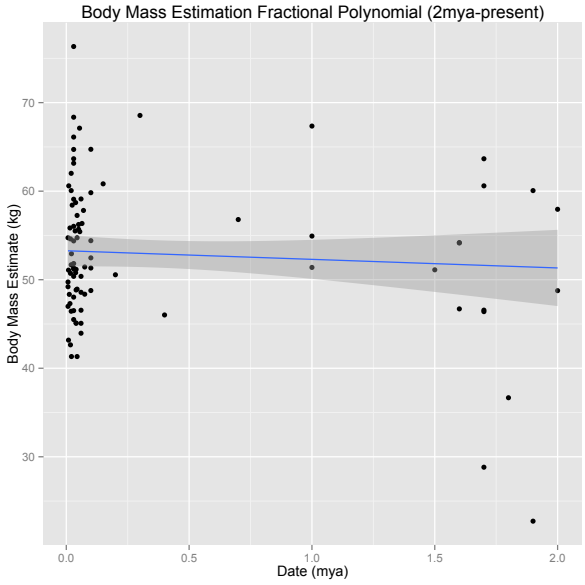

Figure 4.14: Polynomial Fit for Body Mass Estimates (kg) over Time (2mya - present)

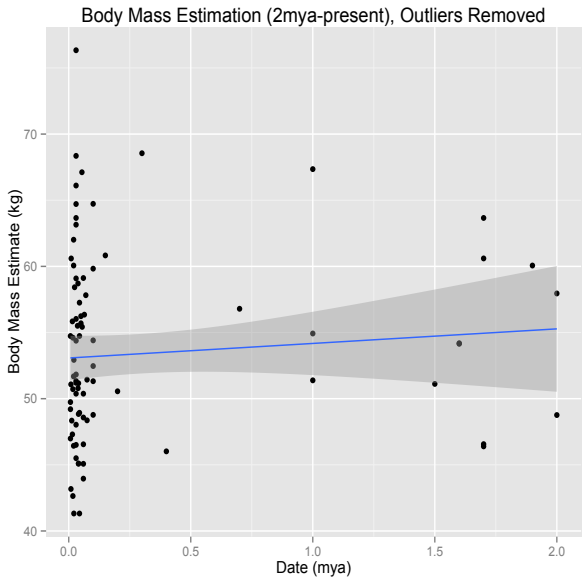

Figure 4.15: Polynomial Fit for Body Mass Estimates (kg) over Time (2mya - present), Outliers Removed

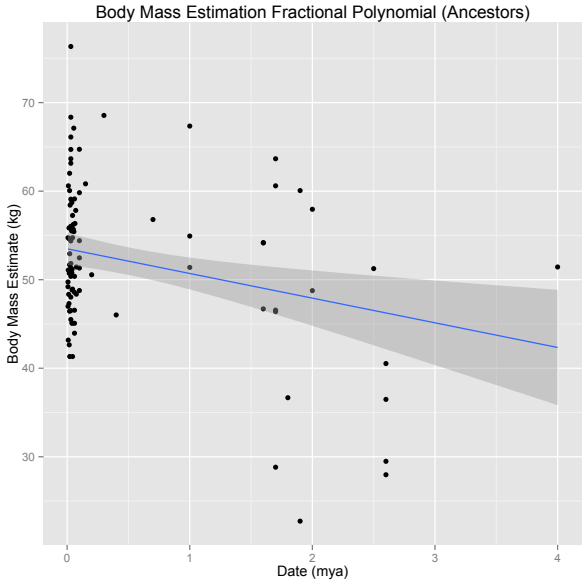

Figure 4.16: Polynomial Fit for Body Mass Estimates (kg) over Time (2mya - present)

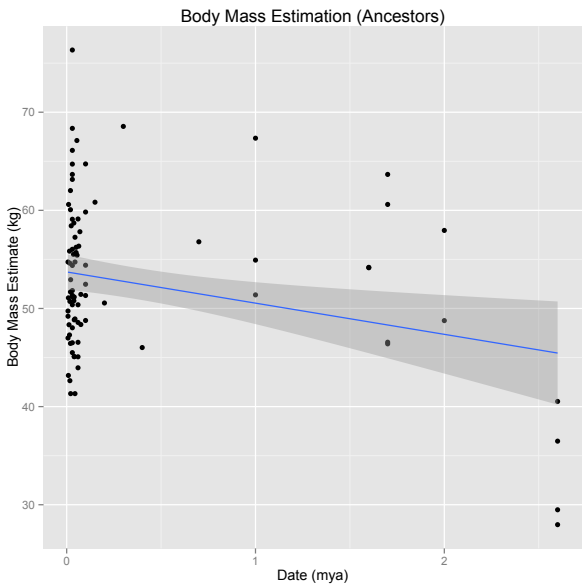

Figure 4.17: Polynomial Fit for Body Mass Estimates (kg) over Time (2mya - present), Outliers Removed

4.2.4 Multivariate Adaptive Regression Splines

Multivariate Adaptive Regression Splines (MARS) are used here to model EV and body mass estimates separately over time. This procedure is a non-parametric form of regression that automatically models non-linearities. Rather than fitting a curve, MARS fits several lines connected at "knots." The knots represent a real slope change. The MARS model is built as

$$\hat{f}(x) = \sum_{i=1}^{k} c_i B_i(x) \tag{4.1}$$

where c_i is a constant and B_i represents "basis functions," in this case the intercept and a hinge function. At its core, MARS is simply a multivariate model that combines several univariate calculations and smoothing. The MARS algorithm includes a loop function that chooses the best placement for a "hinge" or "knot" based on marginal data values. One drawback of this procedure in this analysis is that it is sensitive to measurement errors and knot placement can be difficult in areas of locally high variance. Knot values are given as part of the output from MARS analysis. The slopes of lines were calculated from (x,y) coordinates of end points of lines estimated with R's "locator()" function. The x coordinate of the knots are calculated as part of the MARS analysis, but the y coordinate must be estimated.

Figure 4.18 plots the MARS for EV for the entire sample. Knots are placed at dates of 2.2 mya and 0.4 mya. The slopes of the lines between knots quantify both the direction and rate of change. All slopes

are technically negative, but positive if time is considered progressing towards 0. The time period between 3.2 mya (the earliest included specimens) and the knot at 2.2 mya has the flattest slope (-0.07). The slope increases to -1.32 between 2.2 mya and 0.4 mya, but the steepest slope (-3.199) occurs between 0.4 mya and present.

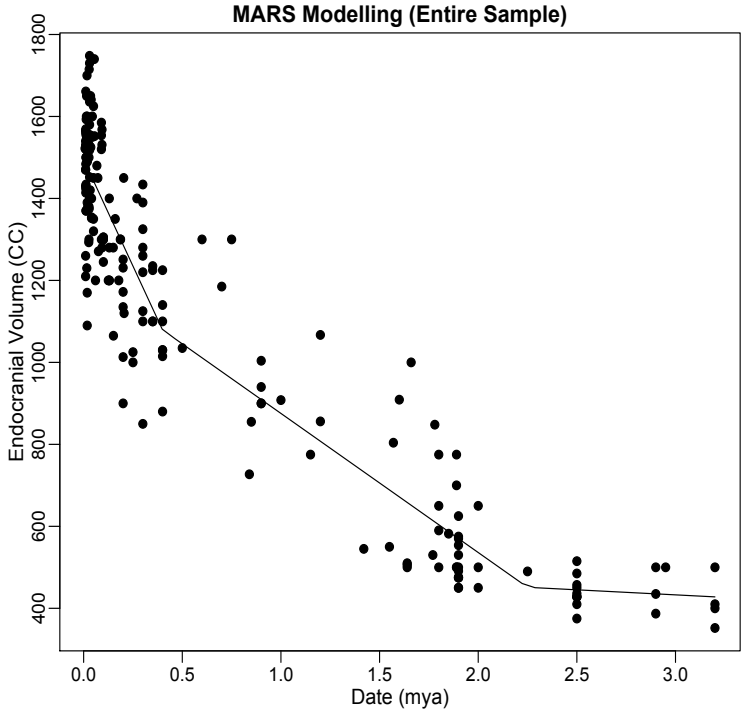

Figure 4.18: Multivariate Adaptive Regression Spline—Endocranial Volume (CC) over time (Entire Sample)

The summary plot in Figure 4.19 shows the model selection and residuals and also identifies the top three outliers. There is some scatter in the residuals, indicating higher variance in the larger cranial capacities. This is not unexpected given the higher values and the greater sample size. In this sample the outliers are Sambungmacan 3, Sangiran 31, and Minatogawa 4. Sambungmacan 3 is an outlier in 3 of 4 MARS analyses. Its EV is 900cc and it dates to 0.2 mya. Minatogawa 4 dates to 0.018 mya and has an EV of 1090. It is an outlier in all of the MARS analyses. These remains have previously been described as small in body size and brain size (Suzuki and Hanihara, 1982). Sangiran 31 is the only outlier in any MARS analysis that is larger than expected, although this is not unanticipated from a specimen originally described as "Meganthropus" (Von Koenigswald, 1973). This specimen is an incomplete skull but consists of most of the calotte so the reconstruction of the EV is considered fairly accurate.

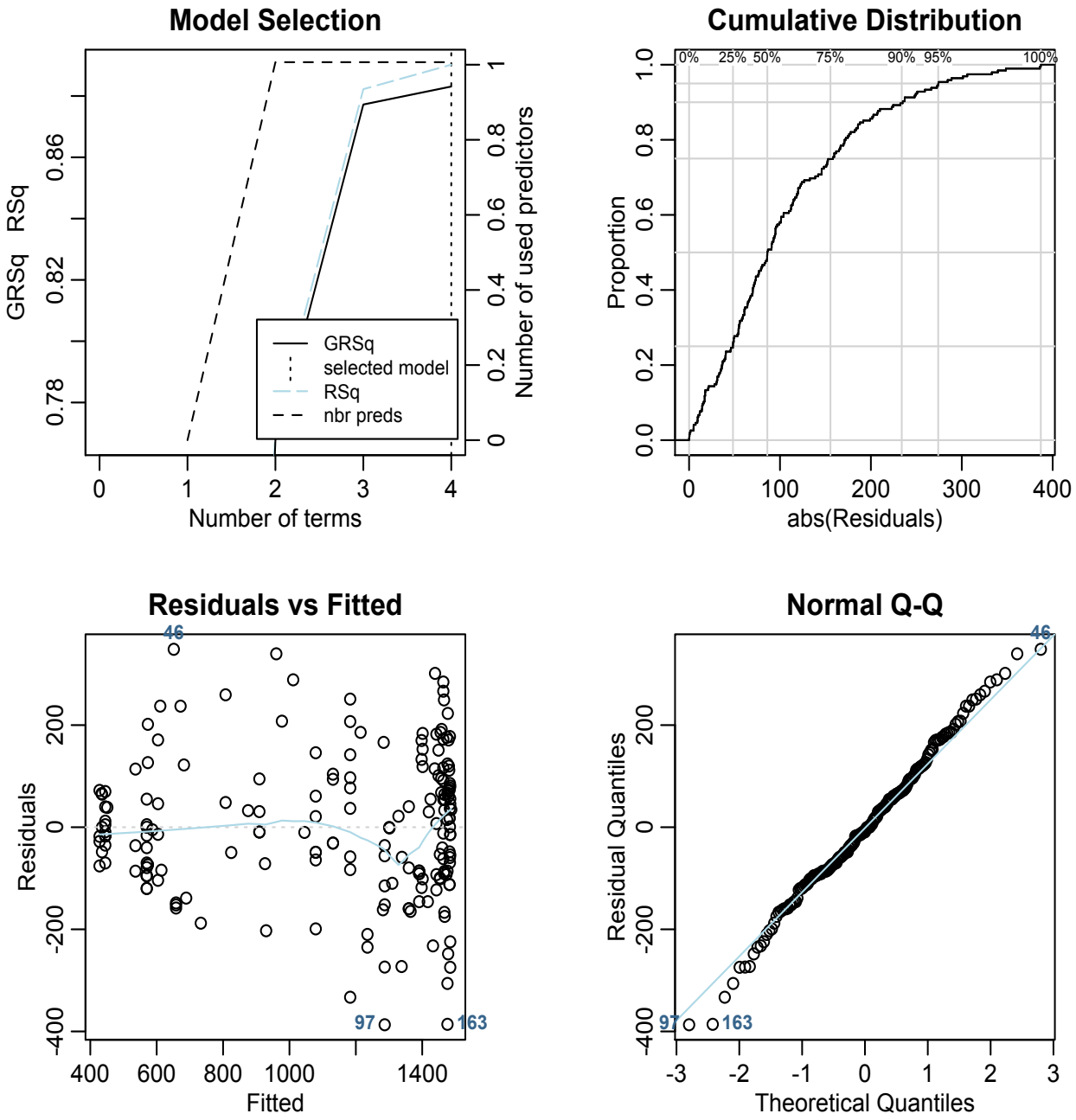

Figure 4.19: Summary of Multivariate Adaptive Regression Spline—Endocranial Volume (CC) over time (Entire Sample)

The pattern changes when the dates are limited to 2 mya—present, depicted in Figure 4.20. The data set for this analysis is Table 3.7. In this case knots were placed at 1.78 mya and 0.2 mya. In contrast to the first plot (entire sample), there is a steep slope (-3.14) leading to the first knot at 1.78 mya. The longest

linear section is between 1.78 mya and 0.2 mya, and the slope is also the flattest (-0.499). The period from 0.2 mya has the steepest slope (-3.26) as in Figure 4.18.

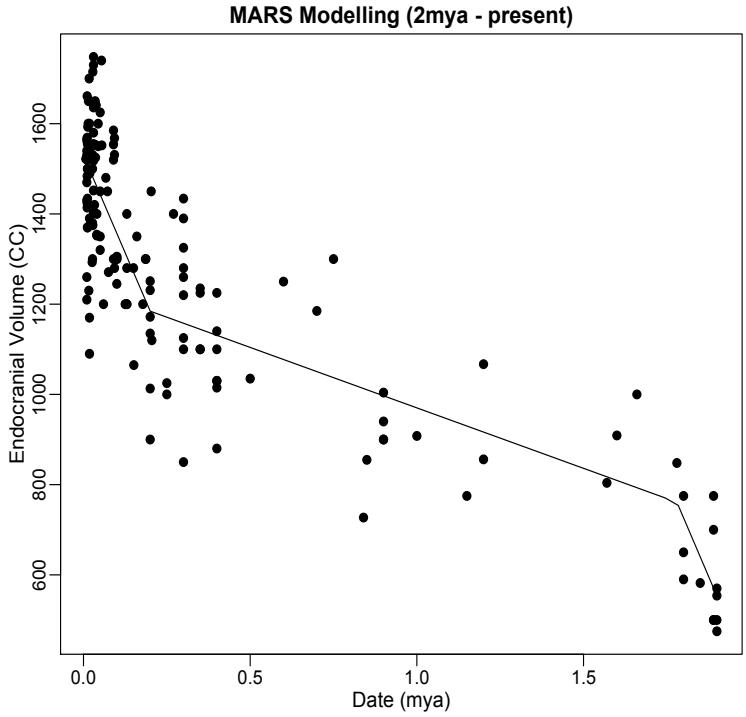

Figure 4.20: Multivariate Adaptive Regression Spline—Endocranial Volume (CC) over time (Entire Sample)

The summary plot in Figure 4.21 identifies the top three outliers as Zhoukoudian IV, Minatogawa 2, and Minatogawa 4. The published EV of Zhoukoudian IV is only 850cc with a date of 0.3 mya. Other specimens in this time period range from 1100cc—1434cc. It is notable however, that there are geographical differences between Zhoukoudian IV and its contemporaries. All other specimens dated to 0.3 mya are from Europe (Atapuerca, Petralona, Reilingen, Steinheim, Swanscombe, Narmada). Minatogawa 2 and 4 date to 0.018 mya and have EVs of 1170cc and 1090cc, respectively. Contemporaneous specimens, including Minatogawa 1 have EVs ranging from 1390cc–1600cc. As stated above, the Minatogawa specimens are known for having small body and brain sizes.

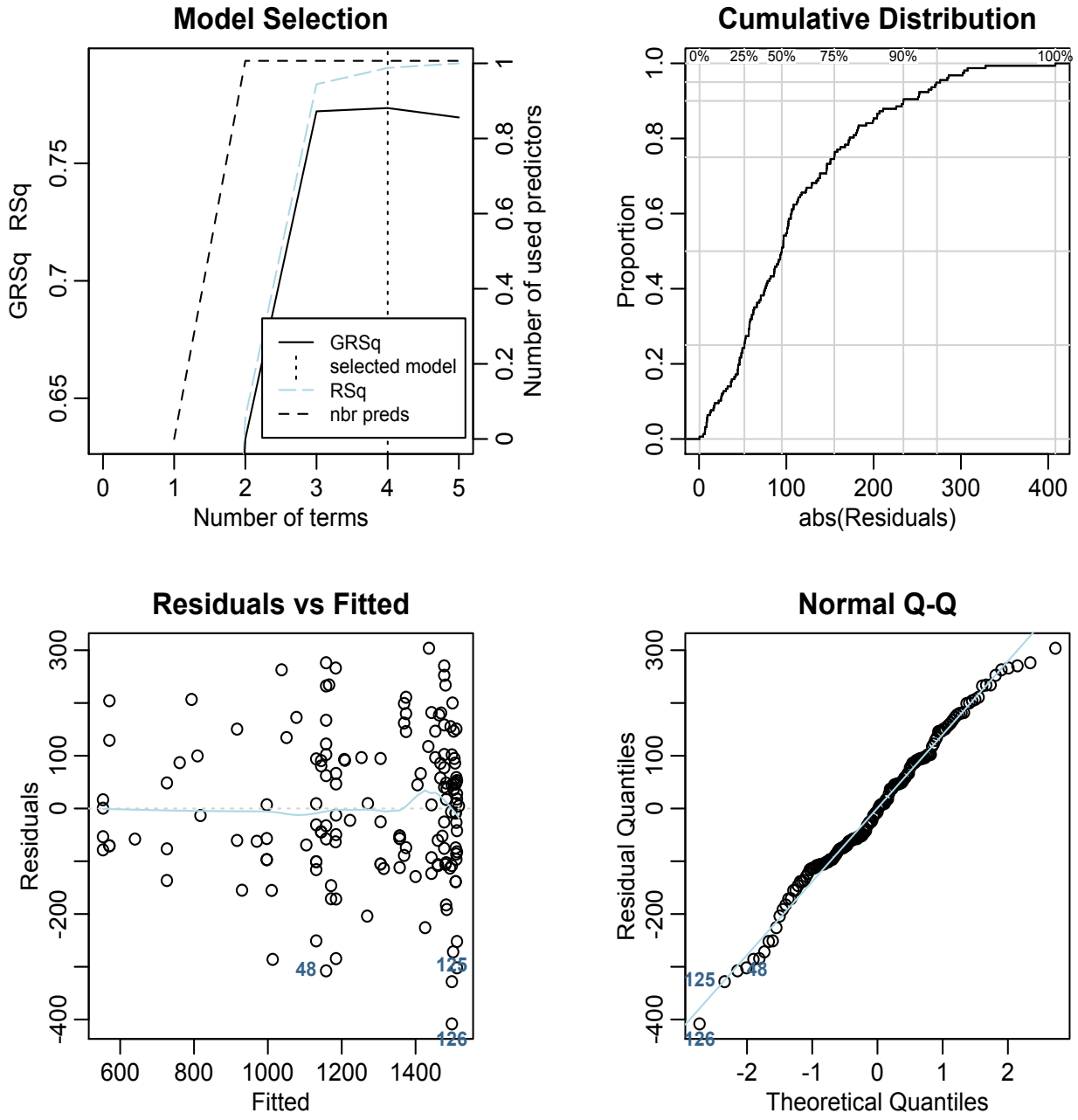

Figure 4.21: Multivariate Adaptive Regression Spline—Endocranial Volume (CC) over time (2 mya—present)

The data set for the third MARS analysis is in Table 3.8. This data set begins at 2.9 mya with *Australopithecus africanus*. It attempts to model the change in brain size through the purported ancestral lineage of *Homo sapiens*. This lineage includes *Australopithecus africanus*, *Homo habilis*, *Homo erectus/erectus*, and

Homo sapiens. Absent an argument for removal, *Homo neanderthalensis* remains in the sample. MARS results are in Figure 4.22.

This MARS analysis differs from the previous analyses in that it places only one knot and it falls at 0.3 mya. The slope between 2.9 mya and 0.3 mya is -0.755. From 0.3 mya to present the slope increases to -3.02.

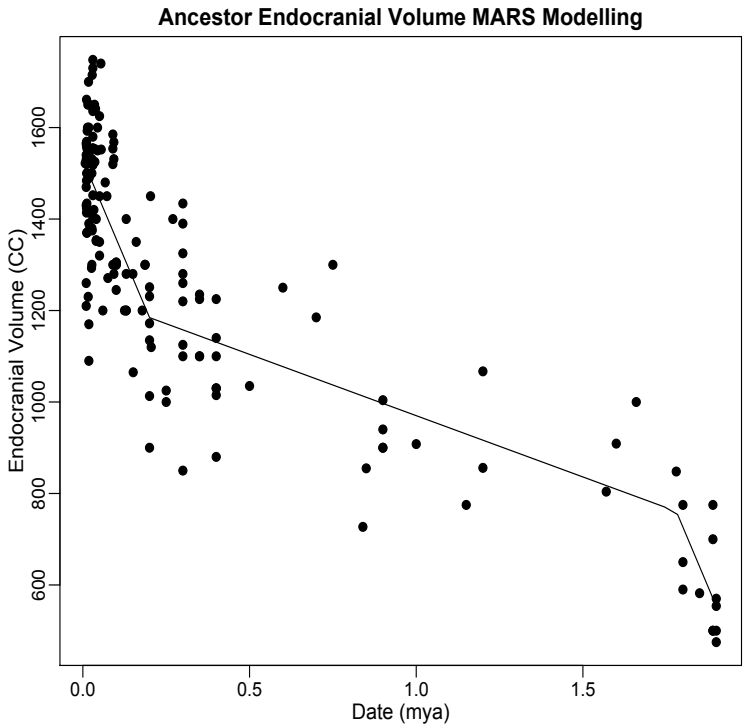

Figure 4.22: Multivariate Adaptive Regression Spline—Endocranial Volume (CC) over time (Ancestors)

The summary plot in Figure 4.23 identifies the top three outliers as Sambungmacan 3, Minatogawa 2, and Minatogawa 4. The modelling shows increased variance as with the previous models.

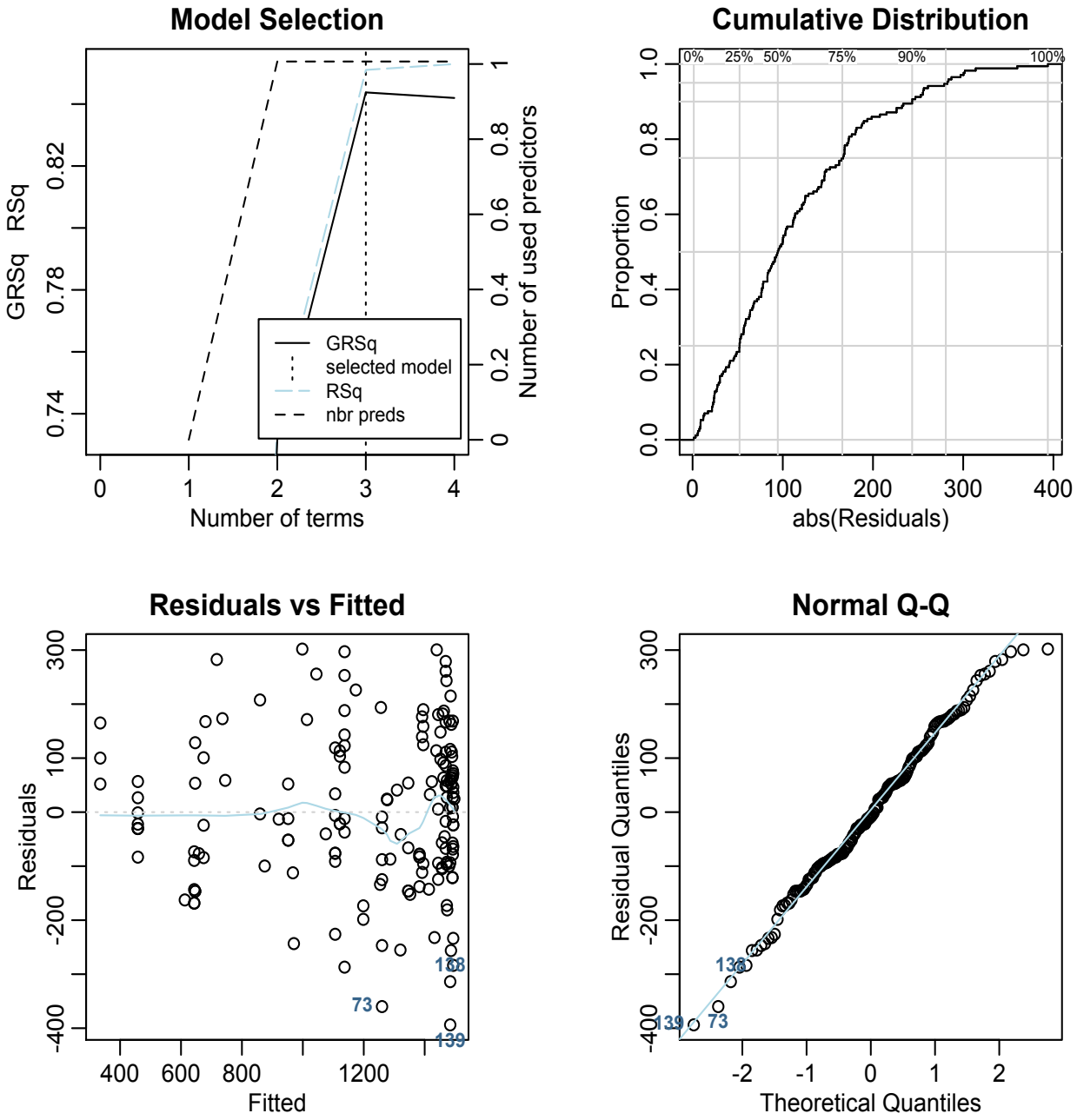

Figure 4.23: Multivariate Adaptive Regression Spline—Endocranial Volume (CC) over time (Ancestors)

The data set for the fourth MARS analysis is the "Ancestral" set found in Table 3.8 but with *Homo neanderthalensis* removed. Removing the Neanderthals does little to change the results, seen in Figure 4.24. The one knot is slightly later at 0.25 mya; the slope between 2.9 mya and 0.25 mya is somewhat flatter (-0.635) and the slope between 0.25 mya and the present is steeper (-3.56).

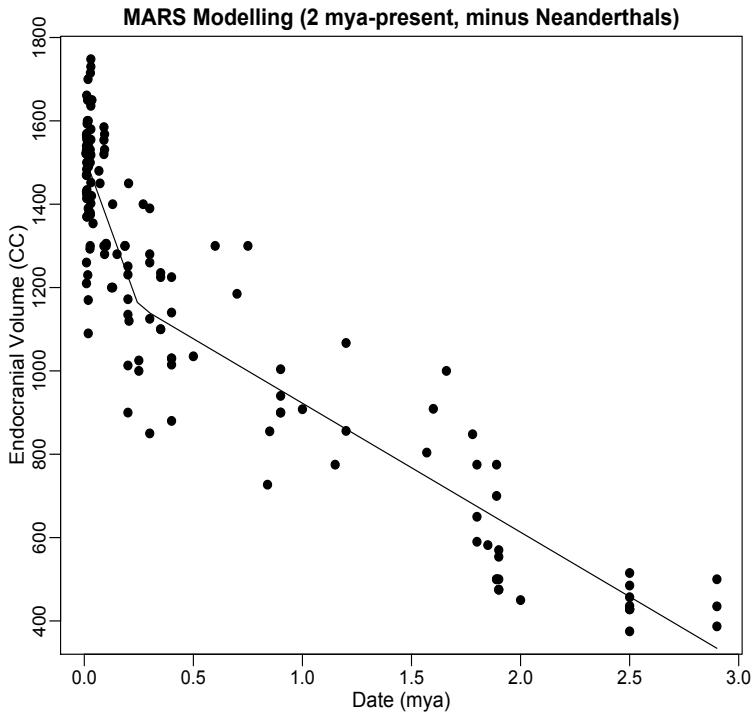

Figure 4.24: Multivariate Adaptive Regression Spline—Endocranial Volume (CC) over time (2mya-present, Neanderthals Removed)

The summary plot in Figure 4.25 identifies the the same top three outliers as the previous sample: Sambungmacan 3, Minatogawa 2, and Minatogawa 4.

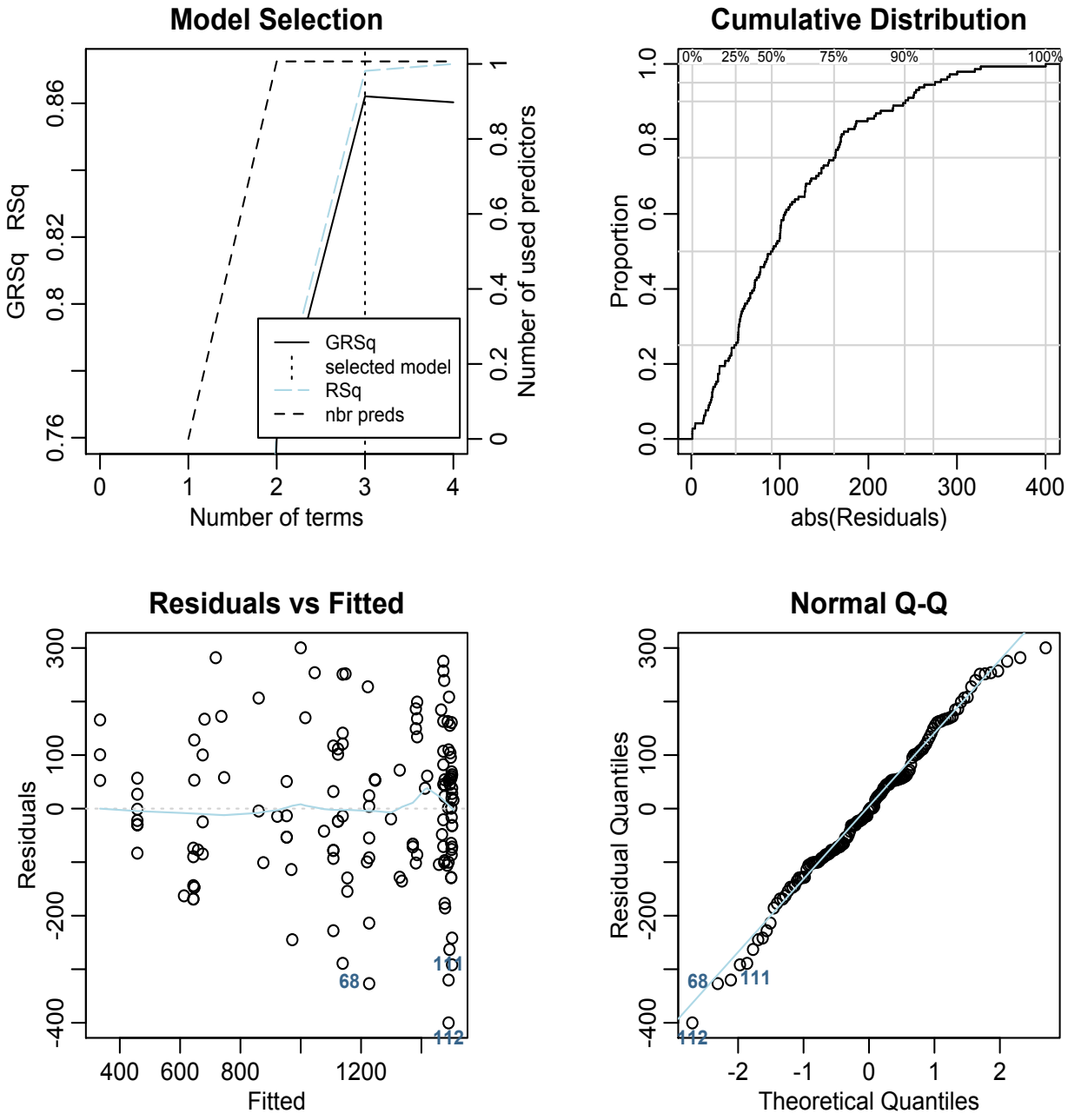

Figure 4.25: Multivariate Adaptive Regression Spline—Endocranial Volume (CC) over time (2 mya - present, Neanderthals Removed)

Figure 4.26 is the MARS analysis for the entire sample and shows a pattern of decreasing body mass between 4.4 mya and 2.6 mya. The slope between the earliest specimen and the first knot at 2.6 mya is 1.81. Between 2.6 mya and the second knot at 1.0 mya the slope is steeper (-2.55) and indicates a trend of

increasing body size. After 1.0 mya this model shows body mass evening out with a slope of 0.

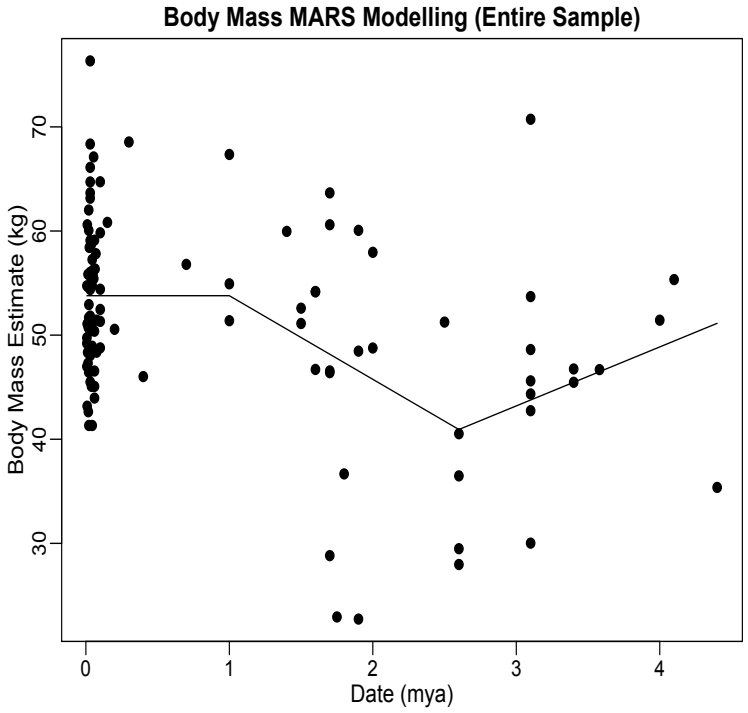

Figure 4.26: Multivariate Adaptive Regression Spline—Body Mass Estimates (kg) over time (Entire Sample)

The model fit and top 3 outliers are shown in Figure 4.27. The three outliers are AL 438-1 (3.1 mya; 70 kg), KNM-ER 1592 (1.9 mya; 60 kg), and Zinjanthropus (1.75 mya; 23 kg). Comparing this model selection to those for the EVs indicates the nature of the differences in the data sets. First, body mass has to be statistically estimated from postcranial skeletal material. Although most measures of EV involve some kind of estimation it is not usually statistical estimation. I specifically excluded any EVs from the literature that were statistically estimated. Secondly, sampling and sample size are an issue for body mass estimation. There are many more available/preserved recent specimens.

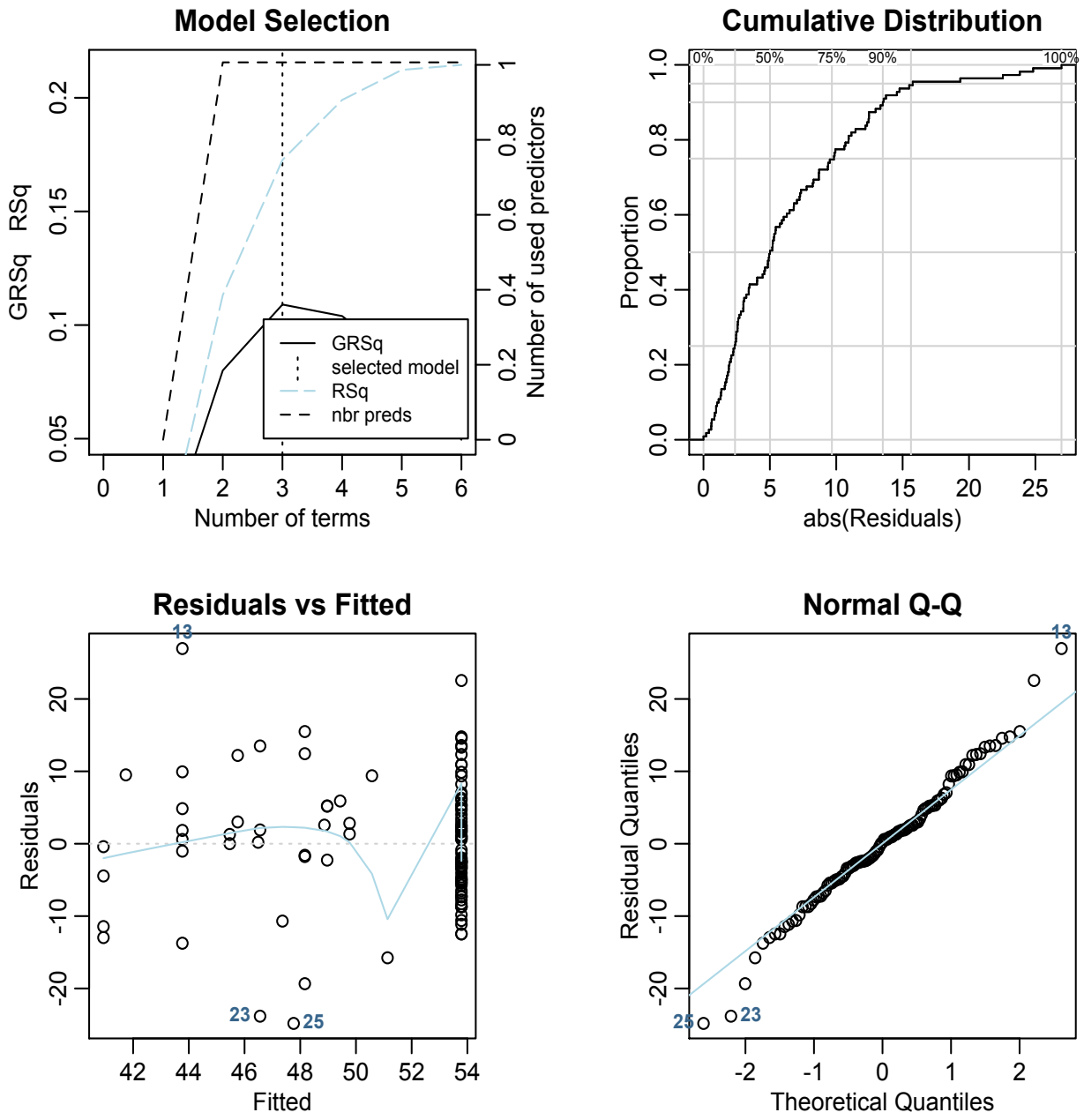

Figure 4.27: Multivariate Adaptive Regression Spline—Body Mass Estimates (kg) over time (Entire Sample)

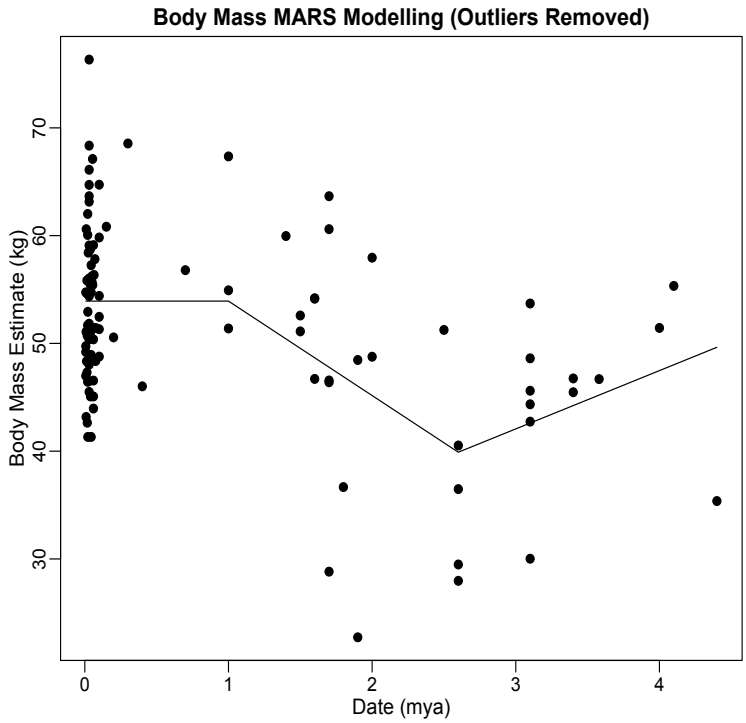

Figure 4.28: Multivariate Adaptive Regression Spline—Body Mass Estimates (kg) over time (Entire Sample), Outliers Removed

In Figure 4.28 the outliers are removed; this does not change the model. The knots are in the same place and the slopes are the same. There is still quite a bit of scatter around the modelled line and the variation in body size estimates is clear. Removal of the three outliers slightly improves the fit of the model (Figure 4.29).

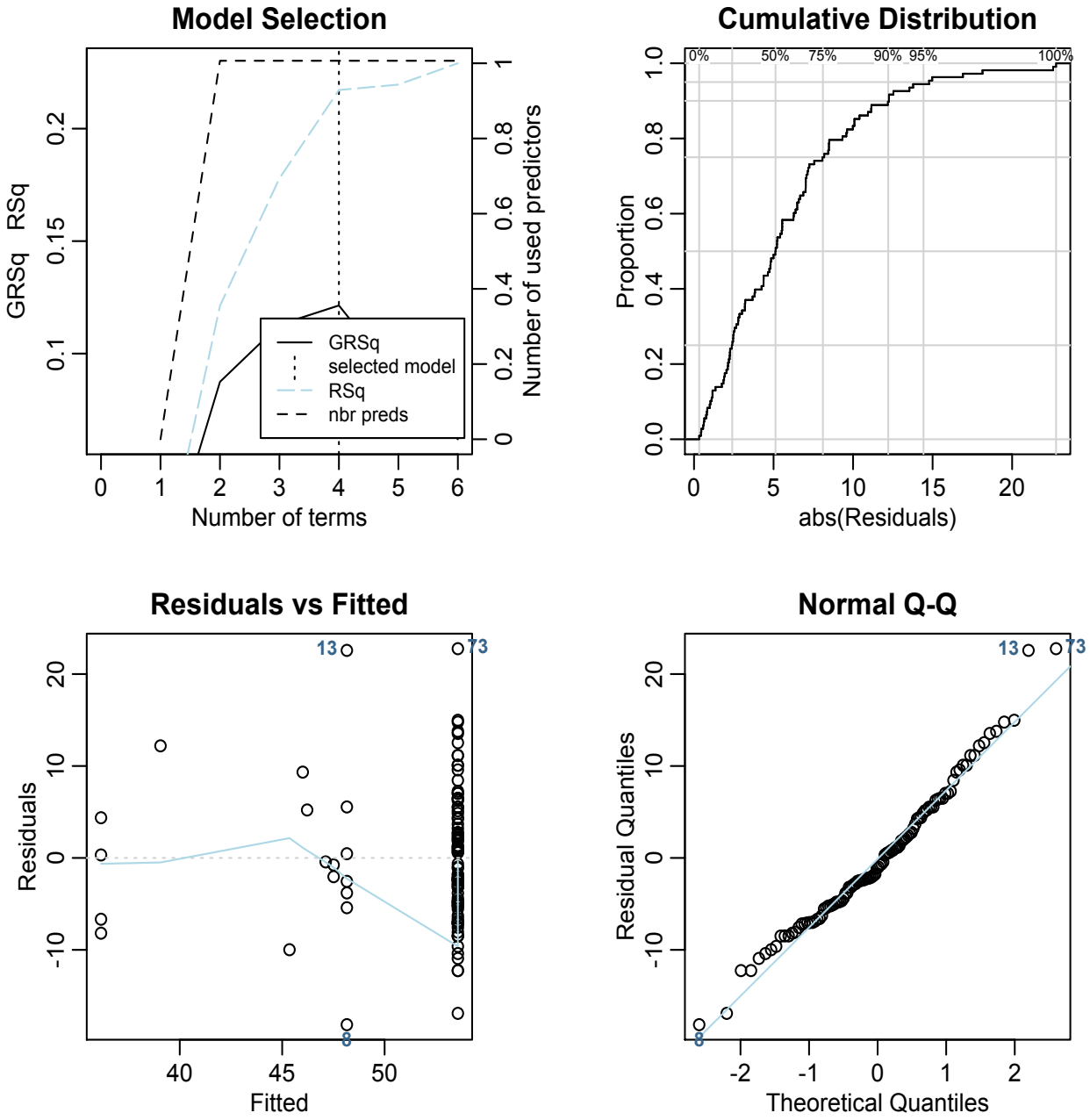

Figure 4.29: Multivariate Adaptive Regression Spline—Body Mass Estimates (kg) over time (Entire Sample), Outliers Removed

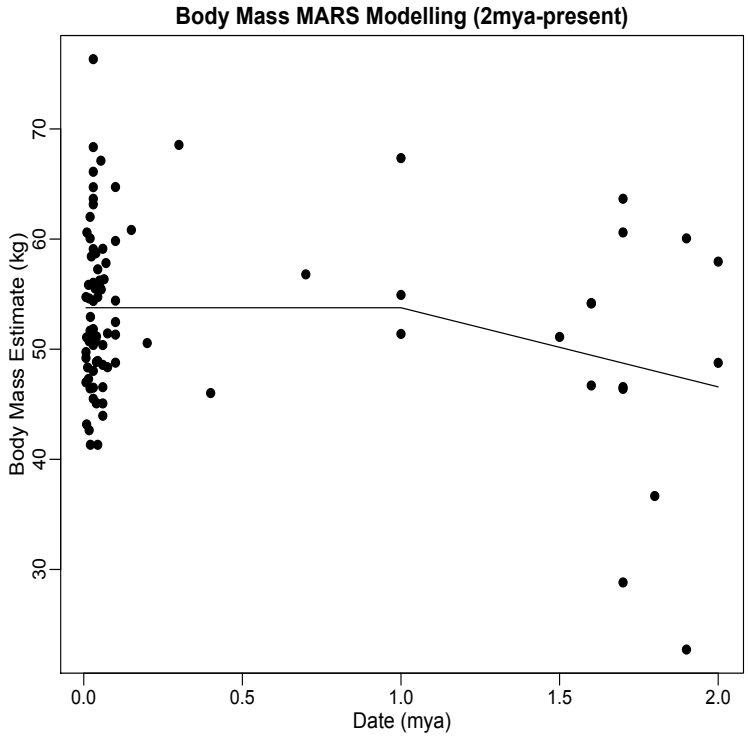

Figure 4.30: Multivariate Adaptive Regression Spline—Body Mass Estimates (kg) over time (2 mya—present)

When only *Homo* specimens are included (see Table 3.4) the MARS analysis has only one knot that falls at 1.0 mya. The slope between 2.0 mya and 1.0 mya is -1.86 and, as in the previous sample, the slope from 1.0 mya to present is 0. The three outliers identified in Figure 4.31 are SKX 2045 (1.9 mya, 23kg), Dmanisis 3901 (1.7 mya, 29kg), and Baousso de Torre I (0.03 mya, 76kg).

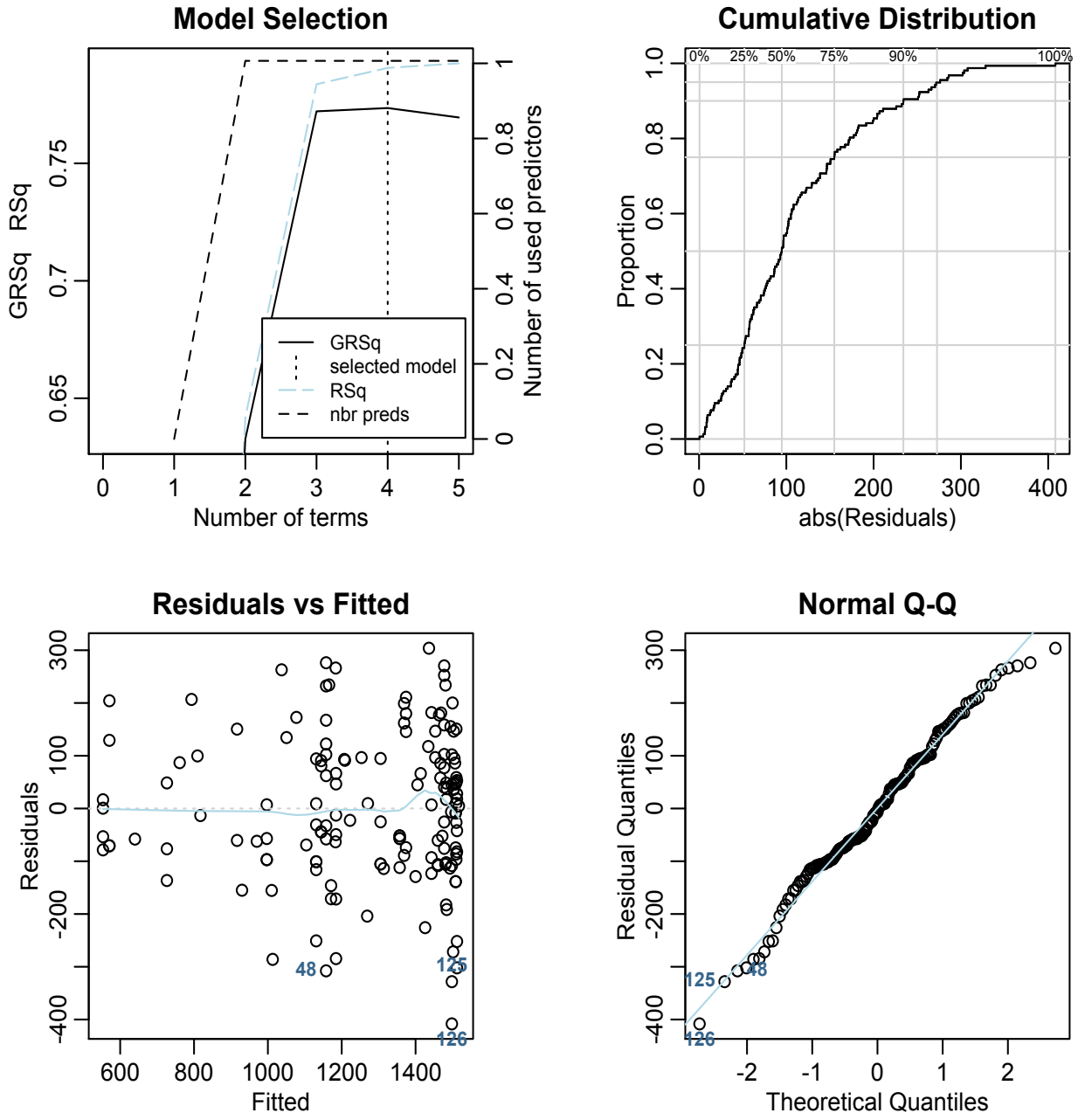

Figure 4.31: Multivariate Adaptive Regression Spline—Body Mass Estimates (kg) over time (2 mya—present)

The inclusion of only *Homo* specimens greatly improves the fit of the model and the residuals (Figure 4.31). All three outliers are small, but are nearly on the line of equivalency. They are identified here because MARS automatically names the top three outliers.

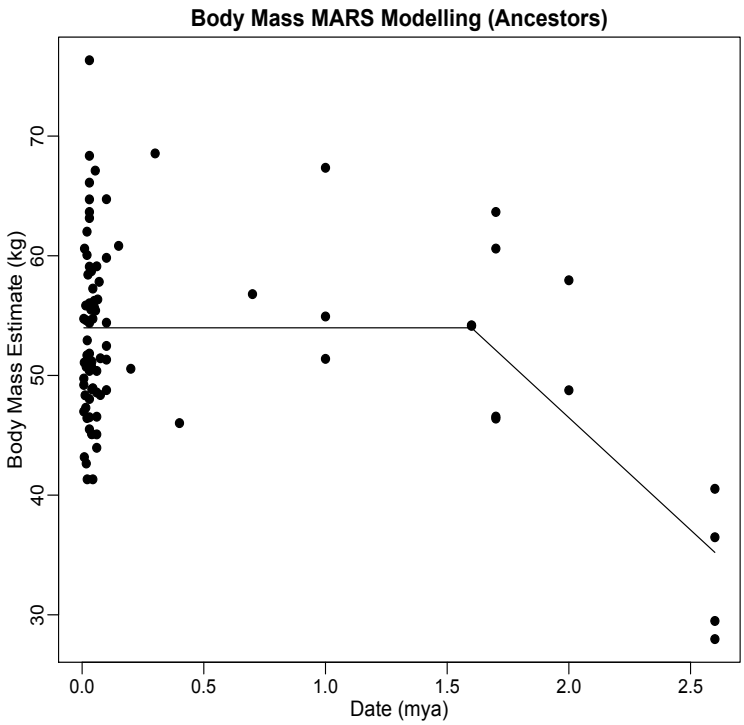

Figure 4.32: Multivariate Adaptive Regression Spline—Body Mass Estimates (kg) over time (Purported Ancestors and *Homo*)

When body mass estimates for Purported Ancestors (see Table 3.5) are subjected to MARS analyses the outcome is very similar to the *Homo*-only analysis. Figure 4.32 shows one knot at 1.0 mya. The slope is not quite as steep at -1.244.

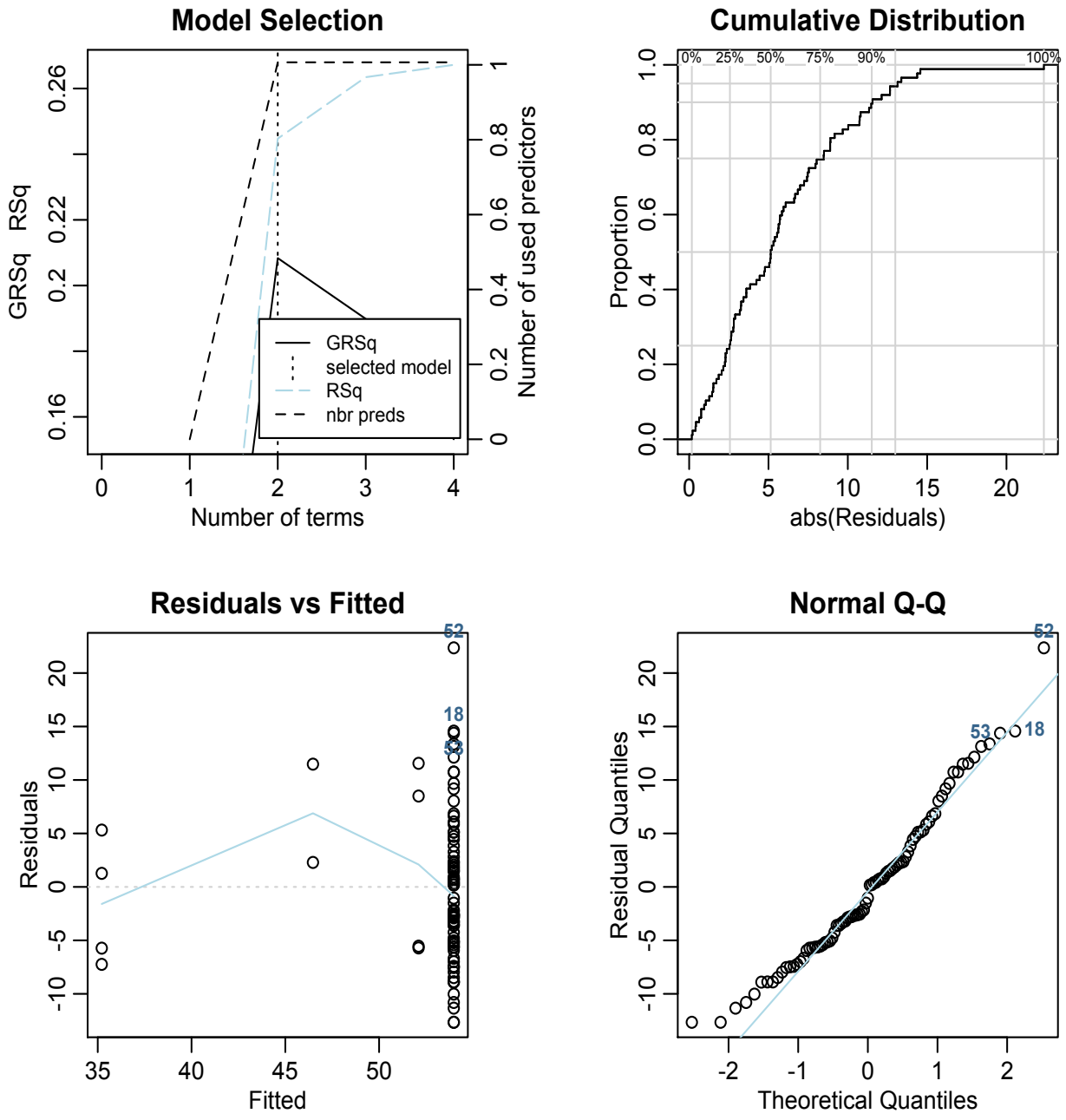

Figure 4.33: Multivariate Adaptive Regression Spline—Body Mass Estimates (kg) over time (Purported Ancestors and *Homo*))

There are three outliers (see Figure 4.33).One is Broken Hill (Kabwe) from 0.3 mya, with an estimated body mass of 68 kg. Both specimens from Baousso de Torre are also outliers. They date to 0.03 mya; specimens I and II have estimated body masses of 76 kg and 68 kg, respectively.

Chapter 5

Discussion and Conclusions

These analyses depict two important aspects of biology—brain size and body size—changing over time. Both brains and bodies have increased in size over time but to state it that way is a gross oversimplification. These analyses show the rate and timing of size changes for brains and bodies differ in important ways.

Brain size shows an upward trend over time but that trend is not steady. Regardless of which sample is used there is a steep increase within the past 0.4 mya. Analyzing subsamples provides some insight to what was happening with brain size before 0.4 mya. In the analysis of the entire sample, which includes *Australopithecus afarensis* and several species of *Paranthropus* there is a barely perceptible increase in brain size between 3.2 mya and 2.2 mya. Body size was decreasing at this time. Figure 4.26 shows a fairly sharp decrease in body size between 4.4 mya and 2.6 mya. If body size was decreasing and brain size was holding steady, the Australopithecines were experiencing encephalization, not because of changes to the brain, but because of changes to the body. This suggests a lack of genetic covariance between brain size and body size already playing a role 2+ mya. It also argues against the simplicity of Cope's law (Cope, 1885), which suggests that body size increases within an evolutionary lineage. Others (e.g., MacFadden, 1986) contend that Cope's law is too simplistic to explain changes in body size over time.

There is not much literature on the brain:body relationship in Australopithecines, except to characterize them as relatively small bodied and small brained. Most of the focus on encephalization in the literature revolves around *Homo erectus*. The first postcranial evidence of *Homo erectus sensu lato* in my sample is SKX 2045 at 1.9 mya. SKX 2045 is an outlier for small body size (refer to Figure 4.31), possibly reflecting the timing of increasing body size that had just begun around 2.6 mya; this also coincides with the beginning of the Pleistocene.

Ruff et al. (1997) argued for encephalization during the past 0.6 mya, preceded by a period of stasis from at least 1.8 mya to 0.6 mya. The period of perceived stasis is based on encephalization quotients calculated for Early-Middle Pleistocene *Homo*, but the data provided actually only includes encephalization quotients for Early Pleistocene (3.064) based on one specimen and shows no data for encephalization quotients between 1.150 mya and 0.150 mya. My results indicate that when Australopithecines and Paranthropines are excluded

body size increases steadily until it levels off at about 1.0 mya. Brain size shows the same increasing trend, but with a much steeper slope (around -3.0, as opposed to the body size slopes, which are less than -2.0).

In the data sets of just *Homo* or the purported ancestral lineage, brains and bodies are both depicted as increasing over time. The slope for the brain size increase is steeper than for the body size increase. Body size becomes static at 1.0 mya while brain size begins a dramatic increase ca. 0.4 mya.

Taken together, these results suggest a complicated relationship between brain size and body size. Both traits were probably experiencing some direct selection, while also susceptible to indirect selection from the other based on their covariation. As Lande (1979) and others have shown, selection even affects the amount of covariation. The dissimilarities in the change of body size and brain size indicate that their covariation was actively changing during the course of human evolution. More detailed analyses are needed to look at regional or species-level differences. Leigh (1992b) found subtle regional variation in encephalization in *Homo erectus* that was also susceptible to the inclusion or exclusion of individual specimens. Part of the difficultly with analyzing separate species is the lack of reliability of taxonomic assignment. Not only is there quibbling over which specimen belongs to which species, but even how many species exist, and how those species relate to each other.

Another area of clear interest is the scaling, biology, and life history of *Homo floresiensis*, for whom reliable body mass estimates are elusive. As more specimens are unearthed and described perhaps the behavior of brain size:body size covariation in an insular environment can shed light on integration and modularity, or the lack thereof. Grabowski et al. (2011) showed that humans have significantly less hip bone integration than great apes, possibly easing the transition to bipedalism by lowering covariation within the hip, thus reducing evolutionary constraint. This pattern of "evolvability" could extend to more general modules or groups of traits, like the skull and brain size, or skeletal and body size.

Changes in selection on brain size and body size would have been rooted in environmental and life history changes. Referring back to the Expensive Brain Hypothesis (Isler and van Schaik, 2009), many biological and life history changes accompany brain size and body size changes. If we examine the analyses of the entire sample, Australopithecines were experiencing decreasing body size and relative stasis in brain size, producing an overall result of encephalization. This could reflect the prediction of decreased growth to reallocate energy to a larger brain (Isler and van Schaik, 2009). Initially, the energetic reallocation, coupled with emerging bipedalism, better foraging skills, and decreased gut size could have released, rather than driven, encephalization (cf. Aiello, 1997).

As brains got relatively larger compared to bodies it was inevitable that at some point either brains would have to get smaller along with bodies or bodies would have to start getting larger. For biological and

physical reasons (e.g., size of the birth canal), animals with large brains must have relatively large bodies (Isler and van Schaik, 2009). After 2.6 mya the selection for bigger brains could be responsible for driving larger bodies, but brains show positive allometry relative to bodies. These changing phenotypic relationships suggest changing genetic relationships, indicating a different pattern in integration that began to emerge.

The change in integration would have allowed body size to achieve stasis while brain size continued to increase. All MARS results for body size show an actual zero slope after 1.0 mya (Figures 4.26, 4.30, and 4.32); the polynomial (linear) fit shows an increase of less than 10kg over the past 1.0 mya (Figure 4.13). During a period from 1.0 mya to about 0.4 mya (see Figures 4.18, 4.20, and 4.22) body size exhibits stasis while brain size shows a steady but relatively modest increase. Around 0.4 mya, despite continuing stasis in body size, brains began increasing steadily and steeply. This time period (between 0.4 mya–0.3 mya) characterizes (depending on which taxonomy is used) the appearance of *Homo neanderthalensis*, and some would argue *Homo sapiens* (e.g., taxonomic assignment of Salé, Kabwe, etc.). Global temperature also spiked around 0.33 mya (Petit et al., 1999).

These results support the work of Lande (1979) who hypothesized that intense directional selection on brains was possible because of a lack of genetic covariation between brain size and body size. In fact brain size increased dramatically while body size remained static for the past 1.0 mya. This also suggests that previous characterizations of hominins becoming human-like 2 mya is an oversimplification of hominin biology and mechanisms of evolution.

An interesting comparison, requiring more inquiry, is the covariation of gorilla bodies and brains. Gorillas have presumably experienced an opposite effect, with their body growth outpacing brain growth. Interspecific growth comparisons could yield important clues for understanding the relationship of brain size to body size and how both species arrive at their adult size and shape. Gorilla growth is especially intriguing because they are the largest and most sexually dimorphic extant primate (Taylor, 1997), and they have small brains relative to their large body size, especially when compared to other apes and monkeys. Lande (1979) calculated a low correlation between adult brain size and body size in primates, suggesting that this low correlation allowed hominin brains to grow quickly in response to selection without a simultaneous increase in body size. However, if this low correlation applies to all primates, gorillas are notable in that they grow large bodies, possibly in response to selection, without a requisite increase in brain size.

One should use caution interpreting trends over time (Bookstein et al., 1978; Pagel, 2002), particularly when using estimates for fossil hominns (Smith and Jungers, 1997; Uhl et al., 2013). Fractional polynomial analysis of body size fits a straight line over time, regardless of which subsample is used. This highlights the kind of effect hierarchy can have on results (Bookstein et al., 1978). Individual human body growth curves

are polynomial (Leigh, 2001), but this interspecific analysis clearly shows a linear trend in body size increase (or lack thereof). This could be because of the way in which selection is affecting body size. Perhaps, as Lande (1979) predicted, selection is not on adult size (estimated and modelled here), but on ontogenetic mechanisms.

Phylogeny is a concern in these analyses. Some of the taxonomic affiliations of fossil remains are still contested, further limiting confidence in results. There is no reason to believe that fossil hominin phylogeny will become more clear, although the addition of new specimens and even new species (e.g., *Homo floresiensis* and *Australopithecus sediba*) could further resolve our past. One possibility, as suggested by Pagel (2002) is to use computing power to analyze all possible phylogenies. It may be that different phylogenetic possibilities have little influence on the overall trends of brain size and body size in hominins.

Another caution of Bookstein et al. (1978) and others is to avoid the false dichotomy of gradualism *versus* punctuated equilibrium. The MARS analysis shows periods of gradual increase and decrease in body size, as well as periods of stasis. Brain size, similarly, shows an early period of stasis, followed by gradual increase and then rapid increase. These results are consistent with Pagel (2002), who found faster rates of brain size increase in more recent hominins.

The linear nature of body size over time means that it cannot be directly compared with brain size, as was one of the goals of this research. Only general relationships can be discerned, and this is cause for prudence when interpreting their relationship. In all likelihood, a metabolic, biological, and life history change as drastic as hominins experienced was a confluence of many environmental and evolutionary factors. The most interesting result is the mechanism of encephalization in Australopithecines—through decreasing body size. Also unexpected was the long stasis in body size beginning ca. 1 mya. At the root of the brain:body size relationship was hominins' ability to take evolutionary advantage, through lowered constraint, of this confluence.

5.1 Conclusions

The evolutionary history of human brain size and body size is quite complex, as is the evolutionary relationship of the two traits. Unraveling the how and why of current human proportions takes consideration of biology, genetics, life history, and climate. This study gives some traction at least to the quantification of these traits and trends over time. Trends over time can speak to the genetics of these traits—how genetically correlated they may have been at any one time (based on how similar or dissimilar their changes were), which direction selection or drift were taking them or preventing them from going, and based on morphology, how

biology and life history may have been changing too.

Previously, a big challenge has been not merely quantifying the traits over time, but assessing the rates of change. This study aimed to report not only the timing and direction of change but also the rate of change. Fitting straight lines, as in the MARS analysis, helps explain differing rates of change in brains and bodies, indicating changes in covariation between the traits.

Encephalization seems to have proceeded differently in Australopithecines and *Homo*. Body size decreased in Australopithecines while brain size remained static. This was probably a period of significant biological and ecological change for that genus, with the emergence of bipedalism impacting foraging behaviors as well as life history variables (e.g., birth canal size). During this time a lack of covariation between brains and bodies was probably especially important.

Early *Homo* shows a small gradual increase in both brain size and body size, with brain size modestly outpacing body size. This may be related to an increased ability to exploit the environment, a change in diet, or expansion to new environments. The Pleistocene *Homo* sample includes African, Indonesian, and Asian *Homo erectus*, representing quite a bit of morphological and environmental variation.

Around 1 mya body size stopped increasing and ca. 0.4 mya brain size increased rapidly. As with the changes in Australopithecines, this would require a lack of covariation in brain and body size. The driving factor for this rapid increase in body size is unknown, but body size was not under the same intense directional selection.

There is still much to learn and understand about the evolution of human brains and bodies. Better resolution will come with continued discovery and descriptions of new fossil hominin material, as well as better reconstruction and quantification of EV through the use of CT scans. With the current available data and methods it appears that body size and brain size were fairly independent and their relationship was changing (smaller bodies, static brains) until the beginning of the Pleistocene. At that time brains and bodies began to increase in size until about 1.0 mya when body size became static. Brains continued their modest increase until about 0.4 mya when their upward trend intensified until modern humans reached our current, highly encephalized form.

Appendix

Table A1: R and Rx p-values After Removal of Highest Absolute Critical Value

Fossil Specimen	**Date (mya)**	***R* p-value**	***Rx* p-value**
AL 129-1b	3.4	$<$ **0.001**	0.921
AL 137-48a	3.1	0.491	**0.027**
AL 211-1	3.1	**0.046**	$<$ **0.001**
AL 288-1	3.1	$<$ **0.001**	$<$ **0.001**
AL 322-1	3.1	0.796	**0.001**
AL 333-140	3.1	$<$ **0.001**	0.766
AL 333-3	3.1	**0.032**	0.161
AL 333-95	3.1	0.179	0.690
AL 827-1	3.1	**0.005**	**0.004**
KNM-ER 1472	1.9	0.617	**0.014**
KNM-ER 1481	1.9	0.507	**0.005**
KNM-ER 1500d	1.9	**0.003**	$<$ **0.001**
KNM-ER 1503	1.9	**0.037**	**0.001**
KNM-ER 1809	1.9	0.338	**0.004**
KNM-ER 3728	1.9	0.197	$<$ **0.001**
OH 62Y	1.8	0.058	**0.004**
TM 1517	1.75	**0.013**	**0.030**
SK 82	1.7	**0.028**	**0.002**
SK 97	1.7	0.079	**0.016**

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Table A1 – continued from previous page

Fossil Specimen	**Date (mya)**	***R* *p*-value**	***Rx* *p*-value**
KNM-ER 3735A	1.6	0.827	**0.001**
KNM-ER 737	1.6	0.289	0.781
KNM-WT 15000	1.6	**0.001**	0.622
KNM-ER 1463	1.5	< **0.001**	< **0.001**
KNM-ER 993	1.5	**0.002**	**0.014**
KNM-ER 739	1.4	0.708	**0.034**
KNM-ER 6020	1.4	0.151	0.475
Trinil I	1.0	0.714	0.901
Ehringsdorf 5	0.15	0.301	0.527
Skhul V	0.1	**0.010**	0.649
Tabun C1	0.075	0.111	0.333
La Quina 5	0.05	0.413	0.886
La Ferrassie 1	0.038	**0.039**	0.682
Barma Grande I	0.03	**0.024**	0.131
Barma Grande II	0.03	<**0.001**	0.337
CroMagnon I	0.03	0.054	0.185
Paglicci I	0.03	**0.031**	0.487
Predmost III	0.03	0.111	0.487
Predmost IV	0.03	0.418	0.647
Predmost IX	0.03	0.319	0.248
Predmost X	0.03	0.265	0.386
Predmost XIV	0.03	0.195	0.424
San Teodoro 4	0.03	0.526	0.969
Brno 2	0.024	0.053	0.577
Font de foret 1	0.02	0.301	0.778
LB1	0.018	**0.001**	**0.001**
Chancellade	0.017	0.140	0.587
Le Peyrat 5	0.017	0.254	0.964

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Table A1 – continued from previous page

Fossil Specimen	**Date (mya)**	***R* *p*-value**	***Rx* *p*-value**
Obercassel II	0.15	0.128	0.874

Table A2: Allometry Values and z-scores for Fossil Specimens with Significant R p-values After Removal of Highest Absolute Critical Value

Fossil Specimen	***R* *p*-value**	**Allometry values**	**z scores**
AL 129-1b	<0.001	FDTD (-4.516); **FECB (5.215)**	NA
AL 288-1	<0.001	**HML (8.714)**; HHD (-3.925); HECB (-1.111); CapH (-4.108); HAW (-0.259); RHD (0.009); FML (-8.247); FHD (-3.849); FAPST (-2.825); FTST (1.944); FAPMS (-4.312); FDTD (0.290); FECB (6.641); TML (-5.610)	HML (5.810); HHD (-2.082); HECB (-0.889); CapH (-3.596); HAW (-0.356); RHD (-1.062); FML (-2.960); FHD (-2.905); FAPST (-1.685); FTST (2.002); FAPMS (-3.721); FDTD (1.418); FECB (8.850); TML (-2.613)
AL 333-140	<0.001	FDTD (-4.178); **FECB (4.825)**	NA
AL 333-3	0.032	**FML (-2.033)**; FHD (-0.188); FAPST (1.647)	FML (-1.511); FHD (-0.796); FAPST (1.791)
AL 827-1	0.005	FHD (1.669); **FAPST (-2.353)**; FTST (1.93); FAPMS (-0.996)	FHD (0.93); FAPST (-3.273); FTST (2.959); FAPMS (-0.717)
KNM-ER 1500d	0.003	**FML (-2.34)**; FAPST (1.881)	NA
KNM-ER 1503	0.037	**FML (-1.625)**; FAPST (1.306)	NA
SK 82	0.028	FHD (-1.351); FAPST (1.409); **FTST (1.823)**	FHD (-3.1); FAPST (0.084); FTST (2.521)

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Table A2 – continued from previous page

Fossil Specimen	*R p*-value	Allometry values	z scores
KNM-WT 15000	0.001	HMSMin(0.034); HECB (-1.232); **CapH(-3.772)**; UML (1.478); FHD (2.288); FAPST (1.12); FTST (0.642); TML (-0.248)	HMSMin (-0.351); HECB (-1.608); CapH (-4.032); UML (1.174); FHD (1.527); FAPST (1.267); FTST (1.025); TML (0.673)
KNM-ER 1463	<0.001	**FML (-3.249)**; FAPST (2.028); FTST (1.795)	FML (-2.711); FAPST (-0.194); FTST (2.685)
KNM-ER 993	0.002	FML (-2.274); FAPST (0.995); **FTST (2.466)**	FML (-2.654); FAPST (-0.591); FTST (2.989)
Sts 14	<0.001	FAPST (1.282); **FTST (-3.428)**	NA
Skhul V	0.01	**HML (2.593)**; FML (0.84); FTMS (-1.332)	HML (2.333); FML (1.136); FTMS (-1.839)
Barma Grande I	0.024	**FML (1.762)**; FAPST (-1.416)	NA
Barma Grande II	<0.001	**FML (2.997)**; FAPST (-2.409)	NA
LB 1	0.001	HMSMax (0.454); HMSMin (3.106); **FHD (3.155)**; FAPST (-1.308); FTST (0.073); FAPMS (-1.28); FTMS (0.881)	HMSMax (0.527); HMSMin (2.769); FHD (-2.562); FAPST (-1.422); FTST (0.84); FAPMS (-0.465); FTMS (-0.462)

Table A3: Body Mass Estimates (kg) After Removal of Highest Absolute Critical Value

Fossil Specimen	MLE 2.5%	MLE	MLE 97.5%	CC 2.5%	CC	CC 97.5%	IC 2.5%	IC	IC 97.5%
AL 129-1b	6.572	48.407	347.880	51.778	51.788	51.778	32.280	55.085	94.002
AL 137-48a	1.997	9.833	41.033	1.373	9.922	55.060	26.338	44.351	74.683
AL 211-1	0.797	3.770	14.377	0.514	3.780	19.660	22.028	37.012	62.191

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Table A3 – continued from previous page

Fossil Specimen	MLE 2.5%	MLE	MLE 97.5%	CC 2.5%	CC	CC 97.5%	IC 2.5%	IC	IC 97.5%
AL 288-1	NA	0.003	0.003	1.452	1.452	1.452	11.539	27.381	64.974
AL 322-1	0.851	4.447	18.434	0.387	4.499	31.796	23.460	39.564	66.722
AL 333-140	13.078	80.478	523.650	69.198	69.198	69.198	33.827	57.547	97.910
AL 333-3	4.695	19.256	72.432	9.112	20.601	39.686	28.411	47.510	79.480
AL 333-95	6.809	38.778	210.623	6.207	39.172	229.854	31.672	53.703	91.056
AL 827-1	1.205	5.755	22.627	7.400	7.400	7.400	23.931	40.231	67.634
KNM-ER 1472	1.509	7.889	33.976	0.973	7.933	47.339	25.767	43.470	73.336
KNM-ER 1481	1.120	6.057	26.268	0.739	6.123	35.607	24.910	42.062	71.022
KNM-ER 1500d	0.084	0.700	3.633	0.992	0.992	0.992	19.359	33.126	56.682
KNM-ER 1503	0.508	3.150	14.445	0.795	3.589	10.438	23.188	39.299	66.606
KNM-ER 1809	0.573	4.205	22.129	0.384	4.342	28.975	25.140	42.775	72.778
KNM-ER 3728	0.380	2.372	10.753	0.305	2.501	12.446	22.140	37.535	63.635
KNM-ER 1504	4.123	19.180	80.531	3.755	19.601	87.354	28.813	48.462	81.512
OH 62Y	0.501	3.910	21.336	0.684	4.450	17.169	25.176	42.884	73.050
TM 1517	1.9	9.308	38.544	11.227	11.227	11.227	26.092	43.927	73.95
SK 82	1.177	5.362	20.244	2.175	6.168	12.325	23.288	39.075	65.561
SK 97	2.180	9.331	34.648	2.556	10.112	30.396	25.339	42.419	71.012
KNM-ER 3735A	0.846	4.496	18.873	0.519	4.502	26.689	23.611	39.841	67.224
KNM-ER 737	9.789	44.492	197.713	7.920	44.631	242.714	32.173	54.149	91.135
KNM-WT 15000	8.841	36.557	145.710	39.893	39.893	39.893	31.326	52.481	87.923
KNM-ER 1463	0.074	0.711	3.991	1.443	1.443	1.443	20.42	34.967	59.878
KNM-ER 993	0.906	5.782	28.264	49.461	305.886	2501.709	40.837	68.890	73.637
KNM-ER 739	70.418	306.751	1588.730	49.461	305.886	2501.709	40.837	68.890	116.216
KNM-ER 6020	23.104	98.289	441.674	22.480	96.967	454.905	35.668	59.963	100.803
Sts 14	8.106	56.027	387.616	55.957	55.957	55.957	32.687	55.722	94.990
Trinil I	13.448	50.888	191.197	9.584	50.894	267.214	32.915	54.927	91.660
Ehringsdorf 5	29.748	80.697	222.587	24.419	80.293	273.180	37.407	60.828	98.912

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Table A3 – continued from previous page

Fossil Specimen	**MLE 2.5%**	**MLE**	**MLE 97.5%**	**CC 2.5%**	**CC**	**CC 97.5%**	**IC 2.5%**	**IC**	**IC 97.5%**
Skhul V	26.585	73.293	204.638	72.276	72.276	72.276	36.452	59.367	96.688
Tabun C1	11.301	31.059	83.143	11.035	32.181	85.093	29.771	48.363	78.565
La Quina 5	20.445	55.703	151.766	15.603	55.703	198.861	34.267	55.697	90.527
La Ferrassie 1	19.323	84.355	383.741	13.399	84.281	566.508	34.893	58.708	98.772
Barma Grande I	50.398	227.350	1191.606	100.360	208.856	537.273	39.026	65.888	111.238
Barma Grande II	4.784	27.050	139.710	30.809	30.809	30.809	30.490	51.655	87.509
CroMagnon 1	38.692	106.524	302.286	50.572	104.271	228.060	39.703	64.713	105.479
Paglicci I	29.384	79.715	219.775	52.232	78.358	122.011	37.300	60.652	98.624
Predmost III	34.949	93.884	258.106	36.262	92.303	248.342	38.856	63.151	102.614
Predmost IV	14.678	39.549	104.996	10.482	39.756	145.336	31.568	51.200	83.040
Predmost IX	9.747	26.677	70.724	7.406	27.049	91.300	28.651	46.507	75.493
Predmost X	11.137	30.389	80.767	8.934	30.783	99.425	29.591	48.033	77.967
Predmost XIV	14.633	39.797	106.640	12.846	40.138	120.994	31.618	51.337	83.354
San Teodoro 4	18.929	50.561	134.493	12.800	50.620	198.108	33.544	54.383	88.167
Brno 2	24.718	68.483	191.585	33.039	68.009	142.651	35.858	58.422	95.183
Font de foret I	32.188	88.234	247.055	27.965	87.983	286.191	38.084	62.015	100.985
LB1	1.824	5.891	17.010	7.684	7.684	7.684	20.645	33.956	55.853
Chancellade	13.891	37.850	101.392	13.429	38.283	104.757	31.235	50.720	82.358
Le Peyrat 5	19.123	51.384	137.589	15.666	51.475	167.692	33.659	54.608	88.601
Obercassel II	12.517	56.909	259.311	12.860	56.874	252.377	33.162	55.843	94.036

Table A4: R and Rx p-values After Removal of Two Highest Absolute Critical Values

Fossil Specimen	**Date (mya)**	***R* p-value**	***Rx* p-value**
AL 288-1	3.1	$<$ **0.001**	$<$ **0.001**

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Table A4 – continued from previous page

Fossil Specimen	**Date (mya)**	***R* *p*-value**	***Rx* *p*-value**
AL 333-3	3.1	0.107	0.228
AL 827-1	3.1	**0.035**	<**0.001**
SK 82	1.7	**0.038**	**0.004**
KNM-WT 15000	1.6	0.210	0.819
KNM-ER 993	1.5	0.058	0.347
Skhul V	0.1	**0.019**	0.700
Paglicci I	0.03	0.944	0.676
LB1	0.018	<**0.001**	<**0.001**

Table A5: Allometry Values and z-scores for Fossil Specimens with Significant R p-values After Removal of Two Highest Absolute Critical Value

Fossil Specimen	***R* *p*-value**	**Allometry values**	**z scores**
AL 288-1	<0.001	HHD (-2.358); HECB (-0.676); CapH (-3.350); HAW (0.761); RHD (0.428); FML (-3.946); FHD (-2.173); FAPST (-2.041); FTST (2.035); FAPMS (-4.091); FDTD (1.085); **FECB (7.611)**; TML (-4.276)	HHD (-1.638); HECB (-0.489); CapH (-3.283); HAW (0.043); RHD (-0.691); FML (-2.426); FHD (-2.363); FAPST (-1.425); FTST (2.263); FAPMS (-3.476); FDTD (1.734); FECB (9.120); TML (-2.196)
AL 333-3	0.107	FHD (-0.923); FAPST (1.322)	NA
AL 827-1	0.035	FAPST (-0.763); **FTST (2.47)**; FAPMS (0.041)	FAPST (-3.001); FTST (3.515); FAPMS (-0.463)
SK 82	0.038	**FHD (-1.188)**; FAPST (1.701)	NA

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Table A5 – continued from previous page

Fossil Specimen	***R p*-value**	**Allometry values**	**z scores**
KNM-WT 15000	0.21	HMSMin (-0.48); HECB (-2.101); UML (1.08); FHD (1.225); FAPST (0.819); FTST (0.567); TML (-0.323)	HMSMin (-0.775); HECB (-2.267); UML (0.543); FHD (0.713); FAPST (0.814); FTST (0.608); TML (0.093)
KNM-ER 993	0.058	FAPST (-0.664); FTST (1.776)	NA
Skhul V	0.019	**FML (2.095)**; FTMA (-1.041);	NA
Paglicci I	0.994	FML (-0.212); FAPST (-0.195); FTMS (0.182)	FML (-0.393); FAPST (-0.254); FTMS (0.508)
LB1	0.009	HMSMax (0.000); **HMSMin (2.714)**; FAPST (-1.790); FTST (-0.252); FAPMS (-1.672); FTMS (0.182)	HMSMax (0.174); HMSMin (2.541); FAPST (-1.740); FTST (0.591); FAPMS (-0.764); FTMS (-0.666)

Table A6: Body Mass Estimates (kg) after Removal of Two Highest Absolute Critical Values

Fossil Specimen	**MLE 2.5%**	**MLE**	**MLE 97.5%**	**CC 2.5%**	**CC**	**CC 97.5%**	**IC 2.5%**	**IC**	**IC 97.5%**
AL 288-1	NA	0.003	0.003	0.382	0.382	0.382	9.423	21.686	49.908
AL 333-3	5.867	23.090	84.825	6.307	23.590	79.454	29.119	48.615	81.167
AL 827-1	0.194	1.680	9.261	0.309	2.202	6.820	22.845	39.003	66.586
SK 82	1.509	6.676	24.951	2.285	7.227	17.815	24.054	40.315	67.569
KNM-WT 15000	13.145	47.168	167.223	9.682	47.724	225.598	32.582	54.190	90.128
KNM-ER 993	3.762	23.155	126.566	5.515	24.300	90.179	30.111	51.116	86.771
Skhul V	25.688	69.924	192.306	47.780	69.444	102.480	36.150	58.784	95.592
Paglicci I	22.776	70.660	188.355	17.533	70.649	290.785	36.469	59.090	95.742
LB1	1.684	8.039	32.265	10.158	10.158	10.158	25.342	42.614	71.657

Table A7: Allometry Values and z-scores for Fossil Specimens with Significant R p-values After Removal of Three Highest Absolute Critical Value

Fossil Specimen	***R* *p*-value**	**Allometry values**	**z scores**
AL 288-1	<0.001	HHD (-1.749); HECB (0.366); CapH (-2.74) HAW (1.782): RHD (1.019); FML (-3.364); FHD (-0.68); FAPST (-0.708); FTST (2.124); FAPMS (-3.607): FDTD (3.893); TML (-4.294)	HHD (-0.294); HECB (0.766); CapH (-2.309); HAW (1.295); RHD (0.492); FML (-1.238); FHD (-0.751); FAPST (-0.586); FTST (3.041); FAPMS (-2.665); FDTD (2.59): TML (-1.179)
AL 827-1	0.047	FTST (1.68); FAPMS (-1.06)	NA

Table A8: Allometry Values and z-scores for AL 288-1 After Removal of All Values Exceeding Critical Value

Fossil Specimen	***R* *p*-value**	**Allometry values**	**z scores**
AL 288-1	0.547	HHD (-1.081); HECB (0.159); RHD (1.149); FHD (-0.327); FAPST (-0.1); FTST (1.178)	HHD (-1.219); HECB (-0.015); RHD (-0.258); FHD (-1.754); FAPST (-1.186); FTST (2.773)

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